A WORLD OF DECISIONS: HOW CHOICES THROUGHOUT THE ANNUAL CYCLE AFFECT SURVIVAL, CONDITION, AND PERFORMANCE OF A MIGRATORY SHOREBIRD

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A WORLD OF DECISIONS: HOW CHOICES THROUGHOUT THE ANNUAL CYCLE AFFECT SURVIVAL, CONDITION, AND PERFORMANCE OF A MIGRATORY SHOREBIRD

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Migratory birds face a variety of threats and constraints throughout the annual cycle, and events that occur in one season can impact individuals not only within that period, but in subsequent seasons as well. I investigated the consequences of decisions about habitat use and species interactions across the full annual cycle on the survival, condition, and performance of Hudsonian Godwits (*Limosa haemastica*) in Beluga River, Alaska and Chiloé Island, Chile.

On the breeding grounds, I examined how the benefits of a protective nesting association between godwits and the loud and aggressive Mew Gulls (*Larus canus*) varied across time and space. Hudsonian Godwits actively chose to nest within gull colonies, but the advantages were context-dependent. Although godwits experienced higher nest survival within colonies – presumably because gulls dissuaded nest predators from using the area – godwit chicks were more likely to be depredated within colonies. Godwits nesting within colonies were larger (females only) and less attentive (males attended the nest less and gave fewer alarm calls). Nest survival was best explained by individual condition improving with female size within colonies and male size outside of colonies.

Turning to the non-breeding grounds in southern Chile, I assessed the degree to which patch quality, as indicated by density and condition of godwits, was affected by environmental attributes and disturbance from predators and/or human activities. Patch quality was primarily influenced by availability of foraging habitat, foraging success rates, and the responses of godwits to disturbance (i.e., vigilance and agitation). Lastly, I examined cross-seasonal

interactions on individual survival and performance. Godwits had high survival throughout the annual cycle, with the lowest survival estimates during the breeding season and southbound migration. I also found evidence of carry-over, or reversible state, effects on future reproductive performance, with individuals in better condition or using higher quality patches on non-breeding grounds achieving higher reproductive success the following spring. Understanding the interactions among stages of the annual cycle, the relative influence of non-breeding and breeding season factors, and the consequences of individual decisions on survival, condition, and performance will help inform conservation for this rapidly declining species.

BIOGRAPHICAL SKETCH

Rose Swift was born in the Bay Area of California. Her parents, Brian and Karen, instilled a love of the outdoors in her from an early age. Camping when she was three months old and skiing when she was three years old, age was not a limitation to explore wilderness. She took that love for the outdoors with her as she began to explore universities. She went on to attend the University of California, Davis where she graduated with a B.S. in Wildlife, Fish, and Conservation Biology with an emphasis on Wildlife Biology. Her first field position was camping at a remote lake in Alaska for three months. There she not only fell in love with the spectacular landscape, but also became engaged with the bird communities she was seeing. Thanks to her field partner, Scarlett, an old pair of binoculars, and her trusty Sibley guide, she developed a passion for birds. At UC Davis, she engaged in many research projects and developed an honors thesis with Dr. John Wingfield investigating the phenological responses of arctic breeding birds to climate change. From these experiences launched a dream – to follow arctic breeding birds from the breeding grounds south and back north again.

After graduating from UC Davis, Rose went on to work many field positions where she gained a variety of ornithological skills. She worked for several seasons at Hastings Natural History Reserve on Dr. Janis Dickinson's long-term Western Bluebird (*Sialia mexicana*) behavioral ecology study. While there, she began to develop a project looking at the repeatability and heritability of egg size. From there, she flew to New Zealand to assist on a project looking at the breeding biology of North Island Brown Kiwi (*Apteryx mantelli*) where she had the opportunity to explore the biology of the endemic Kiwi Tick (*Ixodes anatis*) with Dr. Sarah Jamieson. From nest-searching in Montana to shorebird banding in California, she began to explore the topics she would choose to study for her graduate work. Soon she

would begin to engage in conversations with professors, ultimately finding her love of birds would send her heading to the Lab of Ornithology at Cornell University.

At Cornell, Rose has been involved in the Natural Resources and Lab of Ornithology communities, and she completed her Master's thesis on nest site selection of Hudsonian Godwits (*Limosa haemastica*). Under the continued guidance of Dr. Amanda Rodewald, she has been able to fulfill her dream to work with a long-distance migratory bird and track a species throughout the year and across the hemisphere for her Ph.D. She will now head westward to the Northern Prairie Wildlife Research Center in North Dakota, where she'll be working as a post-doctoral research ecologist on a joint project with USGS and Colorado State University. There she'll work on building a population model for the threatened Piping Plover (*Charadrius melodus*), spreading her wings once again.

For my family:

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CHAPTER ONE

INTRODUCTION

Every annual cycle consists of a series of stages or discrete periods that are defined by specific events, processes, and challenges, which collectively comprise an individual's life history (McNamara and Houston 2008, Wingfield 2008, Newton 2011). Examples of stages include the pre-alternate molt, spring migration, reproduction, pre-basic molt, and fall migration that make up the annual cycles of many birds (Sherry and Holmes 1995, Newton 2011). During each stage, birds are affected by a wide range of factors, including interactions with other species (e.g., Quinn and Ueta 2008), resource distributions (e.g., van Gils et al. 2006, Alves et al. 2013), predation risk (e.g., Martin 1993, Cresswell and Whitfield 1994), and habitat quality (e.g., Cody 1981, Piersma 2012), although the importance of each may vary across time and space. The responses of individuals to these factors can affect their body condition, survival, and performance within and across seasons. In this way, the annual cycle is a complicated process that is subject to potential seasonal interactions (Harrison et al. 2011, Senner et al. 2015). For most at-risk species, we have only a limited understanding of how the threats facing populations interact across their annual cycles in ways that affect their population dynamics. Traditionally, studies have focused on the breeding season, which can directly influence population dynamics via survival and reproduction, but populations also can be limited by factors occurring at non-breeding and stopover sites.

Throughout the annual cycle, individuals must decide about which habitats to use and for what purpose, how to respond to predators or disturbances, and how to interact with other

species. These decisions are dynamic, highly variable throughout the full annual cycle, and affected by many biotic and abiotic factors throughout the year, as individuals encounter new and unfamiliar stopover sites, breeding habitat, nest sites, and foraging sites during the non-breeding season. Because individuals must balance the cost of current reproduction against survival and future reproduction (Williams 1966), they presumably consider, in some manner, the tradeoffs among risk of predation, body condition, and individual performance in habitat selection in each stage. For example, nest site selection in birds is driven by proximate and ultimate factors that maximize fitness (Hildén 1965). Favorable nest locations provide safety from predators, suitable microclimates, proximity to food resources, and enabling social conditions (Martin 1988, Smith et al. 2007a, Betts et al. 2008). On the non-breeding grounds, individuals prioritize survival and prey availability in habitat selection decisions. Distributions of shorebirds are often correlated with the availability and abundance of prey (e.g., Colwell and Landrum 1993), and predators can strongly influence habitat choices of individuals (Fernández and Lank 2006, Sprague et al. 2008). Individuals may also be excluded from high quality habitats or shift habitat use based on their condition or quality, further complicating our understanding of habitat selection (Ydenberg et al. 2002, Studds and Marra 2005). Our understanding of full annual cycle conservation is limited by our knowledge of decisions made by individuals throughout the year. Here, I investigated the consequences of decisions about habitat use and inter-specific interactions across the full annual cycle on the survival, condition, and performance of Hudsonian Godwits (*Limosa haemastica*) at Beluga River, Alaska and Chiloé Island, Chile.

Decisions during the breeding season:

Nest survival can be influenced by a number of factors including nest age, weather, predator abundance, vegetation, microclimate, and human disturbance (Smith et al. 2007a, Smith and Wilson 2010). Birds can improve the likelihood of successful reproduction by selecting nest sites that minimize predation risk or that have vegetative features linked to nest success (Martin 1998). Across a wide range of species, studies have shown that nest microhabitats are selected non-randomly (Colwell and Oring 1990, Rodrigues 1994, Clark and Shutler 1999, Smith et al. 2007a). Although most studies of nest site selection examine the microhabitat surrounding nests (Martin 1998, Clark and Shutler 1999), nest site selection clearly is also shaped by interactions with other individuals (Tarof and Ratcliffe 2004, Gascoigne and Lipcius 2004), including interactions with conspecific or heterospecific neighbors (Hildén 1965, Fretwell and Lucas 1970, Pitelka et al. 1974, Betts et al. 2008), and the stage of the breeding cycle (e.g., incubation vs. brood-rearing; Blomqvist and Johansson 1995, Wiltermuth et al. 2015). Ultimately, the choice of a nest site must integrate many factors including habitat and community-level interactions that drive nest success.

Predation, either perceived or real, can profoundly affect both the life history evolution (Ricklefs 1969) and more contemporary behaviors, including selection of nest sites (Martin et al. 2000). Birds employ several strategies to avoid predation, including egg or plumage crypsis, as well as the placement of nests in locations that are inaccessible to predators (e.g., islands or cliffs) or within protective associations (Bêty et al. 2002, Nguyen et al. 2003, Iverson 2014). In protective associations, the associate species benefits either from aggressive nest defense by the protector species or from information gleaned from the protector species about the whereabouts of predators (Nuechterlein 1981, Quinn and Ueta 2008). Protective associations thus reduce an

individual's risk of nest predation through community-level interactions. Many species in the Arctic have been found to nest near protector species such as owls, raptors, and gulls (Quinn et al. 2003, Nguyen et al. 2006, Kharitonov et al. 2013). However, the extent to which interactions between species are positive or negative can be a function of the biotic or abiotic context (e.g., 'context-dependent interactions'; Chamberlain et al. 2014), which is largely understudied in protective associations. Because protective associations lessen the risk of predation, they may alter selective pressures on nest survival, especially as related to anti-predator behaviors, nest site characteristics, and the quality of the individuals nesting within an area (Smith et al. 2007b). Therefore, identifying the strategies used to avoid predation and the drivers of nest survival is essential to understand reproductive performance.

Decisions during the non-breeding season:

During the non-breeding season, individuals must balance the risks and rewards associated with different habitats as they try to meet their two primary needs – survival and accumulation of sufficient reserves to fuel migration back to the breeding grounds. Individuals must choose among sites that vary widely in food quality, predation risk, and human disturbances (Hilton et al. 1999, Pettifor et al. 2000, Duijns et al. 2009), but individuals often face the dilemma of choosing between risky sites with high-quality resources or safe sites with low-quality resources (Piersma 2012, McArthur et al. 2014). These decisions determine the extent to which they are exposed to risks and rewards, with serious consequences for survival and condition.

The degree to which the quality of foraging patches influences performance and condition may vary among individuals depending upon their vulnerability to different risks.

Individuals foraging in patches with high densities of food have higher intake rates, often spend less time foraging, accumulate mass more quickly, and have better overall body condition (Duijns et al. 2009). Risky environments not only increase risk of mortality but also can compromise body condition if individuals are repeatedly disturbed (Cresswell 2008, Cresswell et al. 2010). Human activity and predators can affect individual performance through changes in scanning behaviors, displacement flights, and opportunity costs of forgone foraging. These behavioral modifications may negatively impact body condition, especially when food is limited, by limiting foraging time (Goss-Custard et al. 2006) and can ultimately affect survival and fitness (Fernández and Lank 2006, Norris and Marra 2007, Cooper et al. 2015). Even when associated with risks, high reward patches can still be beneficial for short periods of time or for individuals in poor body condition (Cresswell 1994). Body condition of foraging individuals is influenced by a wide range of risks and rewards but generally improves with the quality of a patch, sometimes in ways that affect survival and fitness.

Seasonal interactions:

Stages of the annual cycle can interact and affect an individual's probability of survival or reproductive performance at later stages. Seasonal "reversible state effects" are distinguished from direct impacts on survival or reproduction within a single season by affecting the state or condition of individuals transitioning to later seasons in ways that are both reversible and influence fitness (Senner et al. 2015). Reversible state effects have been described for a wide range of taxa, including mammals (Festa-Bianchet 1998, Perryman et al. 2002), reptiles (Broderick et al. 2001), and fish (Bunnell et al. 2007, Kennedy et al. 2008), but they have been most commonly studied in birds (reviewed in Harrison et al. 2011). Access to resources during

non-breeding months is especially well documented to have reversible state effects. One classic example is American Redstarts (*Setophaga ruticulla*), for which individuals that overwinter in high-quality mangrove habitats arrive at the breeding grounds earlier, in better condition, and fledge more young than individuals from poorer-quality scrub habitats (Norris 2005, Tonra et al. 2013, Cooper et al. 2015). Thus, the quality of habitats used throughout the non-breeding season is likely to have a number of reversible state effects for migratory birds, including consequences for individual condition (Battley et al. 2004, Hargitai et al. 2014), migratory timing (Marra et al. 1998, Prop et al. 2003), reproductive success (Norris et al. 2004, Paxton and Moore 2015), and survival rates (Norris and Marra 2007). As such, the conditions and quality of habitat on the non-breeding grounds may influence an individual's future survival probability, condition, and performance.

Research Questions:

- Do Hudsonian Godwits associate with a protector species, and if so, what are the costs and benefits throughout the different stages of the breeding season?
- Do the characteristics of individuals or the drivers of nest survival vary within and outside of a protective nesting association?
- What is the relative influence of foraging success, amount of foraging habitat, landscape and bay characteristics, predation risk, and human disturbances on habitat quality, flock density, and body condition of godwits?
- When are the periods of highest mortality within the annual cycle, and how does non-breeding body condition, habitat quality, and foraging success influence breeding performance?

Study System:

The Hudsonian Godwit (hereafter 'godwit'), breeds in three disjunct regions across the Nearctic and overwinters in the Southern Cone of South America (Walker et al. 2011). An extreme long-distance migrant, Hudsonian Godwits fly ~16,000 km each year and exhibit a cyclical long-leap migration strategy. Here, I focus on a linked population which breeds in south-central Alaska (Beluga River) and over-winters in southern Chile (Senner 2012, Senner et al. 2014). Hudsonian Godwits are one of the fastest declining shorebird species breeding in North America (Smith et al. unpubl. data), and as such, understanding the threats on survival and reproductive performance throughout the annual cycle is prioritized (Senner 2010).

The breeding season has clear implications for population dynamics. Godwits arrive to the breeding grounds synchronously and initiate breeding within a week of arrival. The breeding season is relatively short, spanning the months of May and June, and individuals show high pair and territory fidelity. Godwits breed in open bogs, tundra, and fens dominated by sedges, *Carex* spp., and dwarf birch, *Betula glandulosa/nana* (Swift et al. 2017a). Godwits typically rely on cryptic camouflage for nest protection, and both individuals of the breeding pair incubate and provide brood care (Walker et al. 2011). Adults divide incubation duties with females typically incubating during the day and males at night (Walker et al. 2011, Bulla et al. 2016). Our previous work showed that habitat heterogeneity did not explain spatial aggregations of godwit nests, but may instead be based on social cues (Swift et al. 2017b). Nest survival is high, with >80% of nests successfully hatching, but brood survival can be quite variable (Senner et al. 2017, Swift et al. 2017b). Chapter Two explores the consequences of community-level interactions across both breeding stages (incubation and brood care). Individuals may choose to nest in protective nesting associations, which occur when one or more species benefit directly from occupying nesting

areas defended from predators by a protector species (Quinn and Ueta 2008). Protective nesting associations may relax selection on nest survival within their boundaries or alter the individual characteristics that drive nest survival (Chapter Three).

Individuals spend most of the year on the non-breeding grounds. During the long non-breeding season, godwits must recover from their southward migration, undergo two separate molts, and prepare for their northward migration and breeding season. Godwits typically are encountered when foraging in large flocks on intertidal mudflats along sheltered coastlines in the Chiloé Island region of southern Chile (García-Walther et al. 2017). Godwits usually arrive on the non-breeding grounds in October and are primarily stationary until northbound migration in April (Espinosa et al. 2005). Individuals must assess the potential risks and rewards of alternative patches when deciding on a foraging site (Chapter Four). Upon leaving the non-breeding grounds, godwits undertake an energetically-demanding 10,000 km non-stop flight to the Great Plains region of the United States in as little as 6-7 days before completing a second non-stop flight to reach the Alaskan breeding grounds. Chapter Five addresses how the condition of individuals, as well as the habitat quality where they forage during the non-breeding season, may influence their survival and future reproductive performance. Further, Chapter Five provides the first estimates of seasonal survival for this species.

Thesis Format:

I studied how decisions made by Hudsonian Godwits throughout the annual cycle impact survival, condition, and performance of individuals. The four subsequent chapters of my dissertation are separate manuscripts for publication. In Chapter Two, I examined the context-dependent relationship between Hudsonian Godwits and Mew Gulls (*Larus canus*) breeding in

Beluga River, Alaska. I investigated the costs and benefits of interspecific interactions, which can vary spatially and temporally, to see if the nature of their interactions varied with breeding stage. In Chapter Three, I examined the drivers of Hudsonian Godwit nest survival within and outside of a protective nesting association. In Chapter Four, I explored the relative influence of foraging success, foraging habitat, human disturbances, and predation risk on patch quality for foraging godwits during the non-breeding season. I specifically assessed the risks and rewards for 42 intertidal mudflats on the density and body condition of Hudsonian Godwits. In Chapter Five, I examined the relative influence of the non-breeding season on godwit future reproductive performance through reversible state effects. Additionally, we linked our measures of individual performance with the first seasonal survival analyses for this species. Godwits are declining rapidly throughout their range. Understanding the extent to which decisions made by individuals throughout the annual cycle influence survival, condition, and reproductive performance will inform conservation practitioners about when and where to instigate effective conservation management for godwits.

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CHAPTER TWO

CONTEXT-DEPENDENT COSTS AND BENEFITS OF A HETEROSPECIFIC NESTING ASSOCIATION [1]

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Abstract:

The costs and benefits of interactions among species can vary spatially or temporally, making them context-dependent. For example, benefits associated with nesting near species that deter predators may give way to costs if the association increases the risk of predation during other stages of reproduction. We examined the extent to which the costs and benefits of heterospecific aggregations between a declining shorebird, the Hudsonian Godwit (*Limosa haemastica*), and a potential protector and predator, the Mew Gull (*Larus canus*), varied with breeding stage. Specifically, we assessed the spatial distribution and fate of 43 godwit and 262 gull nests in Beluga, Alaska, from 2014 – 2016. We then evaluated the effect of habitat and proximity to gulls on daily survival rates of 120 godwit nests from 2009 – 2016. We also examined the relationship between the proximity to gulls and survival of godwit chicks to five days old, the period when they are vulnerable to gull predation. Nests of godwits and gulls were significantly clustered across the landscape, a pattern that habitat heterogeneity failed to explain. Hatching success of godwit nests improved with proximity to the gull colony and increasing numbers of gull nests within 200m. In contrast, survival of godwit chicks to five days improved with increasing distance to the gull colony. The costs and benefits that godwits derived from associating with Mew Gulls were thus context-dependent, with benefits pre-hatch and costs post-hatch. Our results show how spatiotemporal variation in species interactions precludes simple generalizations about the nature of their outcomes.

Keywords: Hudsonian Godwit, *Limosa haemastica,* Mew Gull, *Larus canus,* protective nesting association, predation

Introduction:

Heterospecific associations generally arise when participants benefit from living in groups but avoid the costs of competition (Farine et al. 2014). Benefits from aggregations, such as improved access to food, detection of predators, and/or nest defense, derive not only from a group-size effect, but also from the unique or complementary characteristics of each species (Harrison and Whitehouse 2011, Sridhar et al. 2012). Heterospecific associations are widely documented across taxa, including fish (Lukoschek and Mccormick 2000), amphibians (Phelps et al. 2007), mammals (Querouil et al. 2008), and birds (Sridhar et al. 2009). However, studies of these associations are often restricted to specific periods of the year, such as mixed-species foraging flocks that form during the non-breeding season or protective associations occurring during nest incubation in the breeding season (Quinn and Ueta 2008, Sridhar et al. 2009). Understanding the costs and benefits to both the entire assemblage, as well as each species on its own, can inform how these interactions may shift throughout the duration of the association.

One type of heterospecific association is a protective nesting association, which occurs when one or more species benefit directly from occupying nesting areas defended from predators by a protector species (Quinn and Ueta 2008). The protected species can derive a number of benefits from these associations including predator protection, information parasitism, reduced effort defending nests, and improved mate attraction. For example, Western Grebes (*Aechmophorus occidentalis*) react to the alarm calls of Forster's Terns (*Sterna forsteri*) by covering eggs prior to departing the nest, and thereby increasing nest survival (Nuechterlein 1981). Of course, benefits for the protected species may vary among protector species. Yellow Warblers (*Setophaga petechia*) nesting near Gray Catbirds (*Dumetella carolinensis*), for instance, suffer less predation, while those nesting near Red-winged Blackbirds (*Agelaius*

phoeniceus) are parasitized less frequently by Brown-headed Cowbirds (*Molothrus ater*; Clark and Robertson 1979). At the same time, however, protective associations can incur costs that individuals must try to behaviorally mitigate. For example, Red-breasted Geese (*Branta ruficollis*), which suffer from direct predation and harassment when nesting near Peregrine Falcons (*Falco peregrinus*), are able to optimize their fitness by nesting at intermediate distances from falcon nests and thereby minimizing the amount of harassment suffered (Quinn and Kokorev 2002, Quinn and Ueta 2008). Alternatively, some protector species may fail to protect from certain predators. For example, Spotted Sandpipers (*Actitis macularia*) nest within Common Tern (*Sterna hirundo*) colonies for protection from minks (*Mustela vison*), but experience higher egg predation by migrating Ruddy Turnstones (*Arenaria interpres*), which are attracted to the high density of tern eggs (Alberico et al. 1991). That said, if risk varies predictably with distance to a protector species – even if risk differs across life stages (e.g., adult, egg, chick), individuals still may be able to optimize their decisions (Mönkkönen et al. 2007).

The extent to which interactions between species are positive or negative can be a function of the biotic or abiotic context (e.g., 'context-dependent interactions'; Chamberlain et al. 2014). For instance, fluctuations in the population size of a predator's primary prey can drive variation in the magnitude of the pressure predators place on alternative prey (McKinnon et al. 2014). Such scenarios have been reported for heterospecific breeding aggregations. The nesting association between Red Phalaropes (*Phalaropus fulicarius*) and Sabine's Gulls (*Xema sabini*) improves nest success for phalaropes only in years when alternate prey are available for arctic foxes (*Vulpes lagopus*), one of the main predators of phalarope nests. Sabine's Gulls are unable to defend against foxes; thus, nesting within the gull colony provides little protection for phalaropes when the abundance of foxes' primary prey – collard lemmings (*Dicrostonyx*

torquatus) – is low (Smith et al. 2007). Likewise, artificial nests near Long-tailed Skuas (*Stercorarius longicaudus*) gained no survival advantage because skuas depredated clutches in spite of defending their own nests (Larsen and Grundetjern 1997). In this way, context-dependent interactions can have important consequences for population demography and dynamics.

Elucidating how protective associations may change over time can therefore be especially important for uncommon or declining species. The long-distance migratory shorebird, the Hudsonian Godwit (*Limosa haemastica,* hereafter: 'godwits') is one such species for which its conservation is limited by a poor understanding of the cues used to select breeding habitat (Senner 2010). Godwits breed in sedge bogs that are dominated by muskeg interspersed with small ponds, spruce tree islands, and drier upland areas (Walker et al. 2011; Swift et al. 2017a). Though the occurrence and density of breeding godwits varies widely within and across bogs, godwits appear to form semi-permanent clusters within a subset of suitable breeding areas (Swift et al. 2017b). Interestingly, nesting clusters are likely a result of social cues rather than underlying heterogeneity in vegetation or predation risk (Swift et al. 2017b). Our initial observations suggested that godwits may preferentially nest near Mew Gulls (*Larus canus,* hereafter: 'gulls'), a semi-colonial breeder that forms loud, aggressive defensive flocks whenever predators enter the colony (Moskoff and Bevier 2002; RJ Swift personal obs.). Because godwits seldom defend nests (Walker et al. 2011), they potentially have much to gain from nesting near larids, which are common protector species (Quinn and Ueta 2008). At the same time, godwits may have to balance an important cost – gulls are the main predator of godwit chicks (Senner et al. 2017). In this study, we investigated the degree to which the nests of godwits and gulls were

associated and the manner in which costs and benefits of this relationship might vary across different stages of the breeding season.

Methods:

Study area and species:

From 2009 to 2011 and 2014 to 2016, we monitored breeding godwits within an ~8 km^2 area at Beluga River, Alaska (61.21°N, 151.03°W). The study area was divided into two study plots of uninterrupted muskeg bog – North (550 ha) and South (120 ha) – that were separated by ~7 km of unmonitored boreal forest and muskeg bog. From 2014 – 2016, each plot was censused for both godwit and gull nests, although gulls were only partially censused in 2014.

Spatial aggregations of godwit nests are not explained by habitat heterogeneity (Swift et al. 2017b). At Beluga River, godwits breed at a density of five breeding pairs per square kilometer. Godwits seldom defend nests against gulls or other predators during incubation, instead relying on cryptic camouflage (Walker et al. 2011). Mew Gulls are a common, facultatively colonial breeder in both marine and freshwater habitats (Moskoff and Bevier 2002), with nest densities of 10-40 nests per km^2 in our Beluga River study area. Mew Gulls are aggressive toward potential predators, engaging in loud calls and active mobbing. Because they communally defend nests, gull reproductive success correlates with the aggression of a colony (Moskoff and Bevier 2002). Additionally, godwits and gulls nest highly synchronously (nest initiation within one day; RJ Swift unpublished data), despite gulls arriving on the breeding grounds several weeks prior to godwits (eBird 2017).

The community of avian and mammalian predators active at Beluga River is diverse though only a small portion of godwit nests are depredated each year (Walker et al. 2011, Senner

et al. 2017). The main nest predators are red foxes (*Vulpes vulpes*), Common Ravens (*Corvus corax*), and Sandhill Cranes (*Grus canadensis*). Godwit adults are also prone to Northern Harrier (*Circus cyaneus*) predation while incubating. Based on anecdotal observations as well as remains of young godwit chicks (i.e., legs, USFWS metal band, and/or radio) found near active gull nests, we believe that gulls are the main predator of young godwit chicks (Senner et al. 2017), though they rarely depredate eggs (Moskoff and Bevier 2002). In addition to gulls, Great Horned Owls (*Bubo virginianus*), Common Ravens, and red foxes commonly depredate godwit chicks.

Nest distribution and fate:

Once found, nests were marked only with a GPS unit, as we did not physically mark nest locations to avoid associative learning of predator species (Reynolds 1985). For all godwit nests, we estimated hatch date using egg flotation and monitored nests every two to three days until signs of hatching, after which nests were monitored daily (Liebezeit et al. 2007). We typically checked nests by resighting incubating birds with binoculars from 20-30 m away. Adults were flushed weekly (at most) to minimize disturbances that might increase the probability of nest failure, and field teams did not visit nests directly when predators were observed nearby. Although we recorded the locations of all gull nests, only a subset of gull nests were monitored twice weekly. A nest was considered successful if ≥1 egg hatched and chicks successfully left the nest site. We used the presence of young at or near the nest as an indication of nest success. Nest failure was presumed when we found empty nests early in the incubation period and/or destroyed eggs. Due to low rates of nest abandonment and the strong influence of predators on nest survival in this system (Senner et al. 2017), we considered the failure rate of nests in our study to represent the depredation rate as well.

Analyses of point patterns:

Point pattern analyses are the study of the spatial arrangements of points in space, where the datum of interest is the location of the point itself (Diggle 1979, 2003). Point pattern analyses assume a complete census of the study area, and most tests also assume that data are both stationary and isotropic (Fortin and Dale 2005). To comply with the assumption of a complete census, each plot was analyzed separately. Due to consistently small numbers of breeding godwits on South plot (n = 5 each year), spatial analyses are only reported for the North plot. Multi-type spatial patterns were analyzed only for 2015 and 2016, as not all nests were located in 2014. To test the null hypothesis that godwit and gull nests were distributed randomly within our study plots, we used a combination of first- and second-order multi-type point pattern tests. We imported godwit and gull nest data into program R v.3.4.0 (R Core Development Team 2017) and used the SPATSTAT package for point pattern analysis (Baddeley and Turner 2005).

Multi-type tests examine patterns of nest locations between species. Significant associations in first-order nearest neighbor interactions suggest potential local interactions between species from individual nests, which may be indicative of territoriality between species. Significant associations in second-order analyses provide an assessment of potential interactions associated with the total abundance of nests. Evaluations of protective associations among nesting species are more likely to be influenced by the overall abundance of birds rather than the proximity of nearest neighbors, and it is thought that they may be better examined with second-order analyses (Andersen 1992, Diggle 2003). We considered a second-order aggregation of godwit and gull nests as evidence of clustering between species.

For godwit and gull nests in each year, we conducted a first-order multi-type G function analysis as a preliminary tool to assess spatial patterns between the two species' nests. For multi-

type point patterns, the G function estimated the distribution of the distance from a point of type *i* to the nearest point of type *j*, where *i* and *j* indicate the two species. The G function estimated the nearest neighbor distance distribution function G(r) from a point pattern within a defined window and compared it to the theoretical Poisson process.

As our second-order test, we applied multi-type Ripley's K (Ripley 1976, 1988) to detect spatial randomness at successively larger scales based upon the cumulative distribution function (i.e. the number of additional nests within a distance, *r*, of a random nest; Baddeley and Turner 2005). For a multi-type point pattern, the multi-type *K* function counted the expected numbers of points of type *j* within a given distance of a point of type *i*. We derived Ripley's K from the multi-type nest dataset and compared it with the theoretical curve of the Poisson point pattern, which represented complete spatial randomness. We used the linearized form of *K*, $L(r) = (K[r]) - \pi r^2$, to aid in interpretation and to stabilize the variance (Besag 1977, Haase 1995). Here, the expected number of nests in an area with radius *r* is subtracted from *K[r]*, the observed number of nests in a circle with radius *r*. Under complete spatial randomness, the number of nests in a circle follows a Poisson distribution and $L(r) = 0$ for all distances.

Though Ripley's K-function is widely recognized as a useful tool for detecting spatial aggregations, the cumulative character of this statistic often hampers the detection of scale-dependent patterns (Condit et al. 2000, Schurr et al. 2004). If clumping occurs on a relatively small scale, the point density at larger scales will be above average as well because the increasing circular scales are cumulative. Consequently, we also performed the pair-correlation function (PCF; Ripley 1981, Stoyan and Stoyan 1994), which tests for interactions between points (i.e., nests) separated by a distance *r*. Unlike Ripley's K function, which counts all nests contained within a circle, the PCF can be thought of as a circle centered at a given nest, where

the only nests counted are those that lie on the circle boundary (i.e., a ring). The PCF is the probability of observing a pair of nests separated by a distance *r*, divided by the corresponding probability for a Poisson process (Baddeley 2008). Interpretation of the PCF was similar to that of Ripley's K in that values above the upper bounds of the confidence envelope indicate clustering and those below indicate inhibition. For a multi-type point pattern, the multi-type PCF function examines the probability of finding a point of type *i* at location *x* and a point of type *j* at location *y*.

Lastly, we utilized multi-type Ripley's K analyses to evaluate whether godwit nest fate was correlated with its spatial positioning relative to gull nests. For 2016 only, we evaluated successful and failed godwit nests separately relative to all gull nests found. We considered a second-order aggregation of successful godwit nests with all gull nests and second-order inhibition between failed godwit nests and all gull nests as evidence in support of the protective-association hypothesis.

We compared the observed test statistic, $G_{ij}(r)$, $K_{ij}(r)$ or $PCF_{ij}(r)$, against the distribution of $G_{ij}(r)$, $K_{ij}(r)$ or $PCF_{ij}(r)$ from 199 permutations of point patterns based on a Poisson process model with the same density as the observed nests (Ripley 1976, Baddeley and Turner 2005). We graphed the confidence envelope to test for significant deviations from complete spatial randomness in each of our analyses. At each distance, observed $G_{ij}(r)$, $K_{ij}(r)$ or $PCF_{ij}(r)$ below the confidence envelope indicated significant deviations from complete spatial randomness towards regularity or spatial inhibition. Observed $G_{ij}(r)$, $K_{ij}(r)$ or $PCF_{ij}(r)$ above the confidence envelope indicated significant aggregation or clustering. Because variability in user-defined distances for this test can affect the outcome of Ripley's K, we ran each test using the default range as prescribed by SPATSTAT. The recommended range for the distance lags (r) was 0 – 852 m for

the North plot. We initially performed these tests separately by year to verify that the spatial pattern and location of clusters were comparable among years but then pooled across all three years given that our sample sizes were relatively small.

Vegetation parameters:

After godwit nests were no longer active, we measured the habitat at each nest site and a suite of associated random points surrounding the nest. We defined the microhabitat (nest site) scale as the area within a 1-m diameter circle centered on the nest. In each godwit territory, we additionally placed 25 1-m diameter circular plots at randomly selected points. Points were selected from within a 200-m radius of the nest using a random number generator. All points were within the wet sedge dominated bog and study area boundaries.

For each circular plot, we measured the distance to the nearest water body (≥ 2 cm deep) from the center of the circle, and within the plot itself, the percent cover for all species present. From this, we summarized the percentage of the circle covered by shrubs, sedges and grasses, and forbs, as well as the percentage of bare ground (water, mud, or rocks). We also summed the number of plant species present in the circular plot as a metric of species richness (see Swift et al. 2017a, b for more information).

Vegetation analyses:

We used Moran's I test (Moran 1948) to examine if spatial patterning of godwit nest locations was correlated with an underlying spatial pattern in the habitat features used by godwits to choose their nest site. If certain vegetation characteristics drove settlement decisions, then clusters of nests should correspond to patches of especially favorable habitat. We selected focal

vegetation parameters based on previous work (Swift et al. 2017a) showing that godwits selected areas with greater numbers of plant species; more sedge/grass; forb; and tall shrubby cover between 30cm and 1m tall; less bare ground; and were closer to shallow water than random sites. To reduce the number of variables and tests performed, we used the distribution of the results of a principal component analysis (PCA) using these six variables for our Moran's I tests.

To explore spatial autocorrelation, the principal components were tested at three different scales using a different number of distance classes (20, 50, 100) in the freely available software SAM (Rangel et al. 2010), with greater numbers of distance classes representing a finer-scale analysis. Each distance class was defined such that an approximately equal number of pairs of points were considered in each distance class. We determined the significance of Moran's I for each distance class using a randomization procedure with 999 simulations (Fortin and Dale 2005). Vegetation data for nest locations and randomly selected points were analyzed in both a combined dataset and a nests-only dataset. To account for non-independence among distance classes, the significance for each class was assessed using a Bonferroni correction. Moran's I values were then plotted as a correlogram against k distance classes to aid in interpretation (Fortin and Dale 2005). A significant positive Moran's I value indicated a patch of similarly structured vegetation; a significant negative value indicated dissimilar vegetation characteristics and was interpreted as a space between patches (Amico et al. 2008).

Godwit nest survival:

We examined the influence of the gull colony and habitat characteristics on godwit nest survival with mark-recapture analyses. Using all gull nests found from 2014 to 2016 combined, we created a minimum convex polygon for each plot that we defined as the gull colony. For each

godwit nest, we calculated the minimum distance to the gull colony boundary, the number of gull nests within 200 m, and the minimum distance to the nearest gull nest using ArcGIS (ESRI 2015). We also selected six habitat variables known to be used by godwits when choosing their nest sites (Swift et al. 2017a): distance to the closest water body (≥ 2 cm), % tall shrubby cover (between 30 cm and 1 m tall), % bare ground (water, mud, or rocks), % sedge and grass cover, % herbaceous forb cover, and the number of species within the 1-m circle plot.

We used program MARK to estimate daily survival rates (DSRs) of godwit nests in six separate analyses (Dinsmore et al. 2002, Rotella et al. 2004). First, we examined the effects of gull proximity and habitat characteristics on nest DSR for 43 nests monitored from 2014 to 2016. We treated study plot and year as two subsets and initially modeled them separately. Within the subsets we modeled each variable alone as well as in combined habitat and proximity to gulls models. Distance to the gull colony and the nearest gull nest were highly correlated (r^2=0.86) and were therefore not included together in models. We evaluated models using Akaike's information criterion corrected for small sample sizes (AIC_C; Burnham and Anderson 2002), and present beta estimates with standard errors and confidence intervals (CIs). Second, we expanded our analysis to 120 godwit nests found from 2009 – 2011 and 2014 – 2016 and again examined the effects of gull proximity and habitat characteristics on nest DSR. However, because detailed data on gull nests was not collected from 2009 – 2011, our only gull-related metric was the distance to the gull colony boundary, which was presumed to be stable across years. We performed these tests on a combined dataset, by year, and by plot.

Godwit chick survival:

To assess the influence of proximity to the gull colony on the survival of godwit chicks to five days-of-age, we radio-tracked a subset of godwit chicks from successfully hatching nests from 2014 to 2016. Generally, gulls are no longer predators of godwit chicks after day five when godwit chicks become too large a prey item for gulls and are highly mobile (Senner et al. 2017). We randomly selected one or two chicks from each brood to receive a small 0.62 g Holohill radio. We clipped the downy feathers from a small area on each chick's back and attached radios above the uropygial gland with cyanoacrylate glue. We deployed up to 20 radios each year, but not all chicks were located alive within the first five days post-hatching. Each chick was located every two-to-three days until the chick had died or fledged.

We randomly selected one location for each individual within the first five days post-hatch, leading to 29 observations from 25 broods over the three years. For each triangulated location, we calculated its distance to the gull colony, distance to the closest gull nest, number of gull nests within 200 m, and distance to the closest pond in ArcGIS (ESRI 2015). We also calculated the distance to the colony for the nest from which the chick hatched. We then used generalized linear mixed models with a logistic regression to examine the influence of gulls on chick survival to day five, with brood and year as random effects. We evaluated each variable in separate univariate models using AIC_C scores (Burnham and Anderson 2002) in program R (R Core Development Team 2017) with the 'lme4' and 'bbmle' packages (Bates et al. 2015, Bolker 2017).

Results:

Nest Summary:

We found 43 godwit nests from 2014 – 2016, and 120 godwit nests in total from 2009 – 2016. Of these, 83 godwit nests were found within the gull colony (Figure 1). Daily nest survival was high in each year (>97%) for godwits. Apparent nest success (successful nests/total number of nests) averaged 83% for gull nests (n = 151 nests monitored of 252 located; Figure 1).

Godwit and gull nests were spatially clustered on the North plot based on second-order tests (Figure 2; Appendix A Figures A2, A4). Using a nearest neighbor G function, godwit and gull nests were randomly distributed in 2015, 2016, and the combined year dataset (Appendix A Figures A1, A3). However, our second-order analyses suggested a strong aggregation in both 2015 and 2016, as well as the combined years, based on comparison of Ripley's K function with the Poisson point-process null model (Figure 2). Additionally, the PCF test showed similar clustering patterns for 2015, 2016, and the combined years (Appendix A Figures A2, A4). In 2016, successful godwit nests clustered with all gull nests based on the Ripley's K test (Appendix A Figure A5a). However, failed godwit nests also were clustered with all gull nests (Appendix A Figure A5b).

Habitat:

We performed a principal components analysis on the microhabitat characteristics of godwit nests and associated random points from 2014 to 2016 to reduce habitat variables into a smaller set of principal components (PCs) and also to examine the combined effect of multiple habitat variables. At the microhabitat scale, the first two principal components were retained and explained about 55% of the variance. The first principal component (PC1; s.d. 1.45) described a

gradient of vegetation from the number of species (positive values) to habitats dominated by sedges and grasses (negative values; Appendix A Table AI); the second (PC2; s.d. 1.08) separated the distance to water (positive) from habitats characterized by forbs (negative).

Vegetation attributes varied in the degree to which they were spatially autocorrelated (i.e., patchily distributed; Appendix A Table AII). Of the 24 tests of spatial autocorrelation conducted (2 PC variables × 3 distance classes × 2 point subsets (nests and nests + random points) x 2 study plots), 75% (n = 18) yielded no significant autocorrelation (Appendix A Table AII). No patchiness was detected within the nest-only dataset. Significant spatial autocorrelation was detected at distances ranging from 47 – 374 m for the North plot, depending on the number of classes and which PC variables were considered, and no spatial autocorrelation was detected for the South plot. Greater levels of patchiness were detected when all points were included than when restricted to nest locations, suggesting that areas surrounding godwit nests were similar in vegetation structure across the study area. Collectively, these results suggest that vegetation patchiness did not drive the spatial pattern of godwit nests.

Godwit nest survival:

Models that included measures of proximity to gull nests better explained godwit nest survival from 2014 – 2016 than did the constant survival model, while models with habitat measures had the least explanatory power (Appendix A Table AIII). Godwit nests were more likely to succeed as distance to the gull colony decreased (β = -0.008, CI -0.01, -0.003; Figure 3a), and the number of gull nests within 200 m increased (β = 0.29, CI -0.007, 0.59; Figure 3b) – a pattern that persisted whether nests were grouped by year or plot (Appendix A Tables AIV, AV).

We tested the influence of microhabitat variables as well as the distance to the gull colony on godwit nest survival with a linear trend for the 2009 – 2016 dataset. The distance to the gull colony again was the top model (w_i = 0.47), with most habitat measures falling below the null model (Appendix A Table AVI). As the distance to the colony increased, godwit nests were more likely to fail (β = -0.003, CI -0.006, -0.0009; Figure 3c) regardless of whether nests were grouped by plot or year (Appendix A Tables AVII, AVIII).

Godwit chick survival:

Survival of godwit chicks to day five improved with increasing distance to the gull colony (β = 14.29, CI 3.72, 24.85; Appendix A Table AIX). Results were similar whether we used our entire sample or randomly selected one chick from each brood. Eight of fifteen godwit chicks that survived the five-day period moved out of the colony between locations. Seven of twenty-two (32%) godwit chicks born within the colony survived to day five compared to eight of thirteen (62%) godwit chicks born outside the colony. Only eight of nineteen chicks located within the gull colony at any point during the five-day period survived through this period. Whereas, seven of nine chicks located outside the gull colony survived. Nevertheless, godwit chicks moved similar distances per day regardless of whether the chick was located inside or outside the colony (within: 263.6 m, s.d. 201.82, n = 27; outside: 293.97 m, s.d. 177.78, n = 18). However, godwit chicks that were born within the gull colony that survived moved farther per day then predated chicks (survived: 286.0 m, s.d. 220.1, n = 15; predated: 235.6 m, s.d. 181.9, n = 12).

Discussion:

Our results confirmed a heterospecific nesting association between Hudsonian Godwits and Mew Gulls in Beluga River, Alaska, but showed that benefits occurred only during the nesting stage when gulls played an indirect protective role. After hatch, the survival of godwit chicks was negatively associated with their proximity to gulls, which are an important chick predator. The association between gulls and godwits was thus context dependent, and godwits appear to optimize their fitness by adopting a strategy to nest within the gull colony but leave it after hatching. Thus, godwits seem to adaptively respond to a landscape where there is both spatial and temporal variation in suitable nesting habitat and predation risk throughout the breeding season (Mönkkönen et al. 2007, Seppänen et al. 2007).

Although we found that nest survival of godwits was greater near gull colonies, a full demonstration that the nesting association is protective requires three conditions: (1) the ability to recognize potential protectors, (2) active selection of nest sites near protector species rather than simply in similar habitat, and (3) survival benefits exceed the effects of predator swamping (Quinn and Ueta 2008). The association between godwits and gulls meets each of these criteria. First, godwits nested near a species that exhibits loud, defensive behaviors that are easily detected by other species in the community. Protector species are chosen based on both quality and reliability (Larsen and Grundetjern 1997), and they must not affect resource availability for the protected species (Mönkkönen and Forsman 2002). Godwits seem to actively choose to nest near gulls, which are known to nest in association with shorebirds, waterfowl, and jaegers in Europe (Götmark and Andersson 1980, Moskoff and Bevier 2002). Combined, this suggests that godwits recognize gulls as a potential protector species. Second, the association occurs despite differences in microhabitat nesting preferences between the two species (Burger and Gochfeld

1988, Swift et al. 2017a). Mew Gull nests were most commonly found on islands in deep snowmelt ponds that had little vegetation (RJ Swift unpubl. data). While we did not test the spatial distribution or availability of gull breeding habitat, in general, habitat features, such as the pond complexes used by gulls, are randomly distributed across the bog (Swift et al. 2017b). Further, we found that habitat attributes of godwit nest sites (i.e., distance to water, tall shrubby cover) were not major determinants of godwit nest placement or survival; rather, the proximity to the gull colony and the density of nearby gull nests exhibited more influence on godwit nest survival. The aggregation of godwit and gull nests therefore likely has little to do with the spatial distribution of habitats for either gulls or godwits and, instead, is the result of social attraction. Hence, although vegetation characteristics explain some aspect of nesting associations, they do not fully account for the benefits derived from the association (Quinn et al. 2003, Kleindorfer et al. 2009). Third, the density of godwits nesting within gull colonies, though greater than that outside of the colony (average per year: 9.2 nests per km^2 inside vs. 1.2 nests per km^2 outside), was almost certainly too low to result in predator swamping given the abundance and diversity of predators in the system. However, given that other ground nesting birds (e.g., gulls, shorebirds, waterfowl, and passerines) also reach relatively high densities within gull colonies (average per year: 101.1 nests per km^2 inside vs. 12.3 nests per km^2 outside), predator swamping may still play a role. The extent to which these densities may result in swamping is thus unclear, as the higher densities may also attract predators to a prey-rich area.

Several factors may promote a protective association between gulls and godwits. For protective associations to be effective, the breeding seasons of the two species must be synchronous, nest defense must continue throughout the active nesting period, and the protector species must be reliable (Quinn and Ueta 2008). Although we did not directly test whether

godwits can differentiate among potential protectors based on their quality, their nesting distribution suggests that they can. One supporting observation is that godwits do not nest near two other defensive larid species, Arctic Terns (*Sterna paradisaea*) and Bonaparte's Gulls (*Chroicocephalus philadelphia)*, that arrive later to the breeding grounds and thus do not breed in synchrony with godwits (RJ Swift unpubl. data, eBird 2017). In Beluga River, godwits and gulls initiate their nests at approximately the same time (RJ Swift unpubl. data), but gulls arrive to the breeding grounds several weeks earlier and have established territories prior to godwit arrival (RJ Swift unpubl. data; eBird 2017). Because the gull colony is also relatively stable in size and location, and because gulls have high nest site fidelity (Moskoff and Bevier 2002), godwits may be able to use information from previous breeding seasons when choosing nest locations. Furthermore, from 2014 – 2016, the average initiation date for gull nests was within one day of that of godwits (RJ Swift unpubl. data). Highly synchronous nesting and the slightly shorter incubation period of godwits (22 – 23 days) compared with gulls (23 – 27 days) translates into earlier hatch dates for godwits – potentially minimizing the threat of gull predation during the vulnerable chick period. Godwits therefore may be initiating nests as early as possible after arrival to minimize the risk of nesting within the gull colony, while still actively choosing to aggregate with gulls as a potential protector.

Godwits nesting in association with Mew Gulls had 27% higher nest success than did those nesting outside of gull colonies. This benefit is likely the result of active protection from predators by gulls, whereby the defensive behaviors of gulls protect godwit nests when mutual predators such as red foxes (*Vulpes vulpes*) and Common Ravens (*Corvus corax*) are present in the gull colony. High nest survival is a common benefit of protective associations and has been documented in most known cases, but the mechanism for this protection is typically unknown

(Quinn and Ueta 2008). Alternatively, godwits may use the defensive behavior of gulls simply as an early warning system for approaching predators. In this scenario, the gull colony could serve as an 'information center,' with godwits acting as potential information parasites, gleaning information that alerts pairs to the presence of predators, and allowing them to engage in cryptic or defensive behaviors, similar to grebes nesting in tern colonies (Nuechterlein 1981, Burger 1984, Doligez et al. 2002). The effectiveness of protective aggregations, by way of deterring predators, may be more strongly driven by colony size than by species composition. Indeed, gulls experience greater nest success in larger colonies, presumably due to effective mobbing behaviors (Götmark and Andersson 1984). Colonies below a certain threshold density could attract predators, but not offer sufficient protection, and thus increase the likelihood of nest failure for both species, creating an ecological trap (Dwernychuk and Boag 1972, Schlaepfer et al. 2002). Accordingly, we detected the strongest effect on nest distributions with second-order tests, and larger number of gull nests increased godwit nest survival, suggesting that gull colony size was important for godwit nest survival. Thus, further study is needed to identify the mechanisms that drive the protective association between nesting godwits and gulls at Beluga River.

During the chick stage, the benefits of nesting near gulls gave way to costs, with only 42% of chicks located within the colony surviving to day five compared to 70% outside the colony. While predation is a potential cost of nesting near a protector, few studies have shown that protectors can become predators during different breeding stages. For instance, Eurasian Kestrels (*Falco tinnunculus*) protect Eurasian Curlew (*Numenius arquata*) nests, but depredate a small percentage (5%) of curlew chicks each year (Norrdahl et al. 1995). However, curlew chicks are only an incidental prey item of kestrels. Furthermore, large colonies of gulls (over 500

pairs) have been known to completely eliminate cohorts of waterfowl chicks whose parents nested in association with the colony, creating an ecological trap for nesting waterfowl (Dwernychuk and Boag 1972). Therefore, the context-dependent relationship between godwits and gulls may not be unique.

Despite the potential dual nature of heterospecific associations, the predictable spatial variation in predation risk from nesting and/or territorial predators can provide protected species with the opportunity to adaptively respond to the changing nature of these relationships (Thomson et al. 2006, Mönkkönen et al. 2007). For instance, individual godwits may be able to compensate for the trade-off between nest and chick predation risk by nesting at intermediate distances or on the edge of the gull colony (Mönkkönen et al. 2007). Alternatively, godwits could compensate for nesting within a stable, risky environment through brood movements, such as by leading their broods to safer habitats outside of dense gull breeding areas. Brood movements that avoid predator-rich or food-poor areas have been well-studied, including with Kentish plover (*Charadrius alexandrinus*) chicks that show increased survival and growth rates in a non-natal habitat that was food-rich and predator-poor (Kosztolányi et al. 2007). Accordingly, we relocated most godwit broods outside their natal territories and often in areas of the bog with few nesting gulls (RJ Swift personal obs.). Invertebrate prey biomass and habitat attributes vary little across the bog and are therefore unlikely to explain use of these areas (Senner et al. 2017; Swift et al. 2017b). In fact, individuals hatched from nests within and outside of the gull colony moved similar distances each day, suggesting biological constraints on the distances moved. Rather, godwits with surviving broods that survived to five days moved farther each day than those that were predated. Behavioral responses to nesting in risky environments

may thus allow godwits to compensate and increase chick survival despite nesting in close proximity to gulls.

Our study thus provides evidence that Hudsonian Godwits benefit from nesting inside the Mew Gull colony through increased hatching success but bear a cost of lower chick survival due to gull depredation. Based on these findings, we suggest that the nature of interactions between godwits and gulls changes with breeding stage and is, therefore, context-dependent. Our study is among the first to examine the effects of protective associations beyond the nest stage and to document context-dependent interactions based on breeding stage. The costs and benefits of this association are clearly complex, and the lasting benefits (e.g., lifetime fitness) for nesting Hudsonian Godwits associating with Mew Gulls remain unclear and require further study.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Swift et al. (2018).

Swift, RJ, Rodewald, AD, Senner, NR. 2018. Data from: Context-dependent costs and benefits of a heterospecific nesting association. Behavioral Ecology. https://doi.org/10.5061/dryad.m8s2r36.

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TABLES AND FIGURES

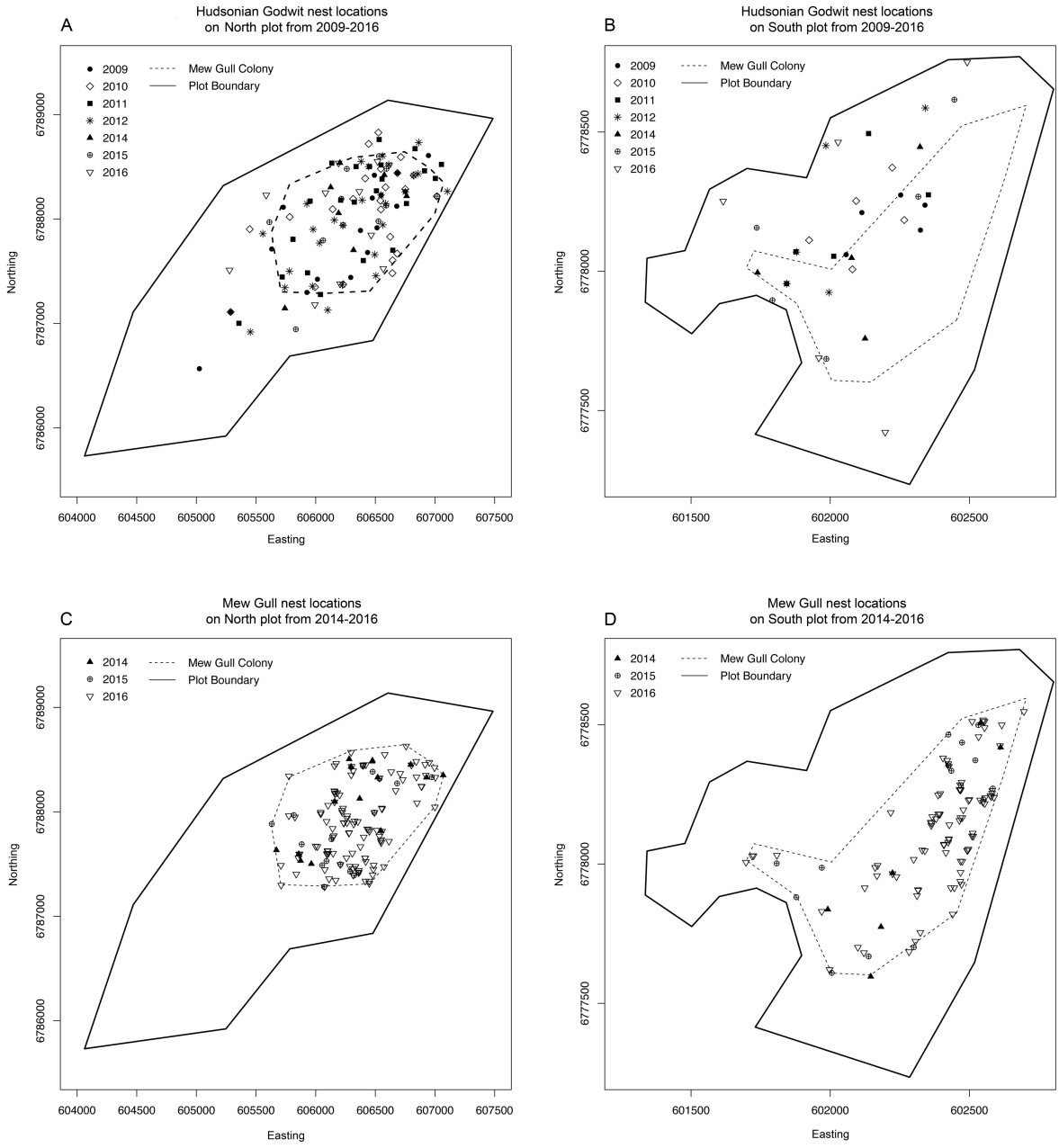
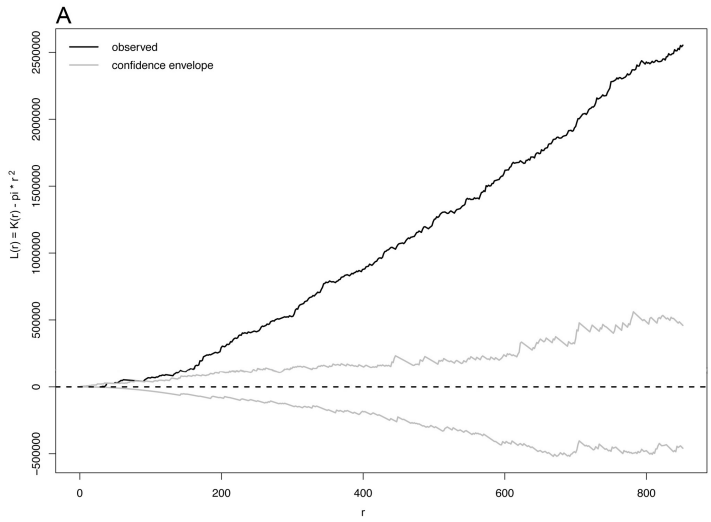


Figure 1. Nest locations, gull colony, and study plot boundary for Hudsonian Godwits (*Limosa haemastica*) and Mew Gulls (*Larus canus*) in Beluga River, Alaska. (A) Hudsonian Godwit nest locations on North plot from 2009 – 2016. (B) Hudsonian Godwit nest locations on South plot from 2009 – 2016. (C) Mew Gull nest locations on North plot from 2014 – 2016. (D) Mew Gull nest locations on South plot from 2014 – 2016. The dashed line shows the Mew Gull colony boundary, and the solid line shows the study plot boundary.

Figure 2. Ripley's K function (transformed to L(r)) for all Hudsonian Godwit (*Limosa haemastica*) and Mew Gull (*Larus canus*) nests found on North plot in 2015 (a), 2016 (b), and combined year dataset (c). The solid black line represents values for the point pattern (observed), dashed black line represent the expectation under complete spatial randomness (theoretical) of the Poisson null model, and the gray lines represent the confidence envelope based on 199 randomizations of a Poisson point process. Values above the upper bounds of the confidence envelope indicate clustering at distance r, and values below the lower bounds indicate inhibition.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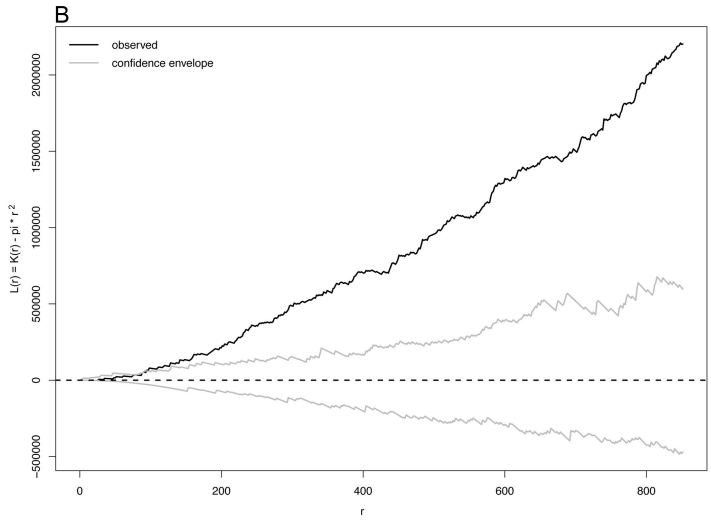
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confidence envelope
L(r) = K(r) - pi * r^2
2000000
1500000
1000000
500000
0
−500000
0
200
400
600
800
r

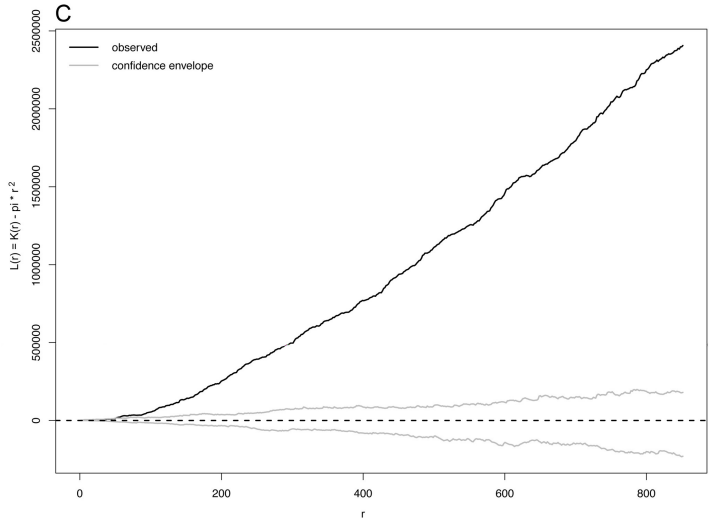
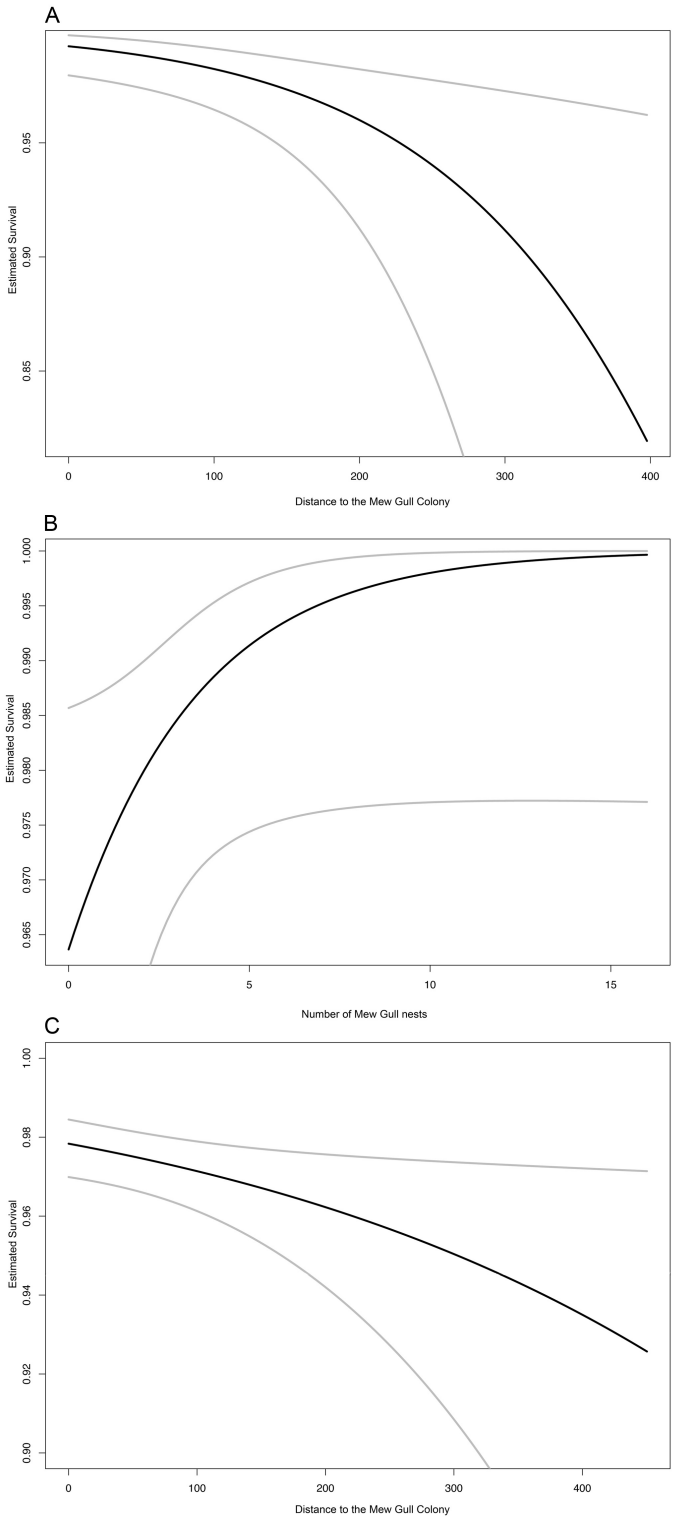

C
observed
confidence envelope
L(r) = K(r) - pi * r^2
2500000
2000000
1500000
1000000
500000
0
0
200
400
600
800
r

Figure 3. Daily survival rates of Hudsonian Godwit (*Limosa haemastica*) nests at Beluga River, Alaska. From 2014 to 2016, survival declined with increasing distance to the Mew Gull (*Larus canus*) colony (a) and increased with increasing numbers of Mew Gull nests within 200 m (b). From 2009 to 2016, daily survival rates of Hudsonian Godwit nests declined with increasing distance to the Mew Gull colony (c). Ninety-five percent confidence intervals shown (gray lines).


A
Estimated Survival
0.85
0.90
0.95
0
100
200
300
400
Distance to the Mew Gull Colony
B
Estimated Survival
0.965
0.970
0.975
0.980
0.985
0.990
0.995
1.000
0
5
10
15
Number of Mew Gull nests
C
Estimated Survival
0.90
0.92
0.94
0.96
0.98
1.00
0
100
200
300
400
Distance to the Mew Gull Colony

APPENDIX A

Table AI. Standard deviation, eigenvectors, and variance explained by principal components (PCs) of microhabitat variables measured at Hudsonian Godwit (*Limosa haemastica*) nests and randomly-selected sites near Beluga River, Alaska.

	Principal components	
	PC1	PC2
Standard deviation	1.45	1.08
Proportion of variance	0.35	0.19
Cumulative proportion of variance	0.35	0.55
Variable loadings		
Distance to water (m)	0.35	0.48
% Bare	-0.27	0.07
% Forb species	0.42	-0.53
% Sedges and grasses	-0.51	-0.21
% Shrubs between 30cm and 1m tall	0.36	0.51
Number of plant species	0.49	-0.44

Table AII. Results of Moran's I tests of spatial autocorrelation for principal components of vegetation features associated with Hudsonian Godwit (*Limosa haemastica*) nests for the North and South plots. Each variable was evaluated using 20, 50, and 100 distance classes and two subsets of point vegetation data: all points and nests only. The significance of Moran's I coefficients for each distance class was evaluated using a Bonferroni correction. When significant spatial autocorrelation was detected at a given distance class, the median distance (m) of that class is reported; "NS" indicates that the result was not significant. When significant spatial autocorrelation was detected for multiple distance classes, the range of the median distance of the closest and farthest distance classes is reported, along with the p-value associated with those classes. The percentage of distance classes with a significant Moran's I value is given as the % significant. The percentage of significant distance classes that had a positive Moran's I value, indicating a cluster, is given as the % positive.

	All points				**Nests only**			
	Dist (m)	% signif	% pos	p-value	Dist (m)	% signif	% pos	p-value
North Plot								
PC1								
20	355	5	100	0.001	NS	NS	NS	NS
50	300-374	4	100	0.001	NS	NS	NS	NS
100	369	1	100	0.001	NS	NS	NS	NS
PC2								
20	84	5	100	0.001	NS	NS	NS	NS
50	47	4	100	0.001	NS	NS	NS	NS
100	108-359	2	100	0.001	NS	NS	NS	NS
South Plot								
PC1								
20	NS	NS	NS	NS	NS	NS	NS	NS
50	NS	NS	NS	NS	NS	NS	NS	NS
100	NS	NS	NS	NS	NS	NS	NS	NS
PC2								
20	NS	NS	NS	NS	NS	NS	NS	NS
50	NS	NS	NS	NS	NS	NS	NS	NS
100	NS	NS	NS	NS	NS	NS	NS	NS

Table AIII. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and proximity to Mew Gulls (*Larus canus;* MEGU). Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for all godwit nests found in 2014 – 2016 at Beluga River, Alaska.

Model	$dAIC_C$	k	Weight
Distance to MEGU colony	0.00	2	0.46
Distance to MEGU colony + number of MEGU nests	1.23	3	0.18
Number of MEGU nests	1.57	2	0.16
Distance to MEGU nest	2.13	2	0.12
Distance to MEGU nest + number of MEGU nests	3.12	3	0.07
Intercept only	4.84	1	0.03
Distance to water + % sedge and grass cover + % tall shrubs + number of species + % forb cover + % bare ground	4.89	6	0.03
Distance to water	5.91	2	0.02
Number of species	6.19	2	0.02
% tall shrubby cover	6.32	2	0.01
% Forb cover	6.82	2	0.01
% Sedge and grass cover	6.85	2	0.01

Table AIV. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and proximity to Mew Gulls (*Larus canus;* MEGU). Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for godwit nests grouped by plot (North and South) found in 2014 – 2016 at Beluga River, Alaska.

Model	$dAIC_C$	k	Weights
Distance to MEGU colony	0.00	2	0.46
Number of MEGU nests	1.57	2	0.20
Distance to MEGU nest	2.13	2	0.16
Intercept only	4.84	1	0.04
Distance to water + % sedge and grass cover + % tall shrubs + number of species + % forb cover + % bare ground	4.89	6	0.04
Distance to water	5.91	2	0.02
Number of species	6.19	2	0.02
% tall shrubby cover	6.32	2	0.02
% Forb cover	6.82	2	0.02
% Sedge and grass cover	6.85	2	0.01

Table AV. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and proximity to Mew Gulls (*Larus canus;* MEGU). Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for godwit nests grouped by year (2014, 2015, 2016).

Model	$dAIC_C$	k	Weights
Distance to MEGU colony	0.00	2	0.46
Number of MEGU nests	1.63	2	0.21
Distance to MEGU nest	2.16	2	0.16
Intercept only	4.86	1	0.04
Distance to water + % sedge and grass cover + % tall shrubs + number of species + % forb cover + % bare ground	4.93	6	0.04
Distance to water	5.92	2	0.02
Number of species	6.20	2	0.02
% tall shrubs	6.34	2	0.02
% Forb cover	6.84	2	0.02
% Sedge and grass cover	6.86	2	0.01

Table AVI. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and proximity to Mew Gulls (*Larus canus*). Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for all godwit nests found in 2009 – 2016.

Model	$dAIC_C$	k	Weights
Distance to gull colony + T	0.00	2	0.47
Number of species + T	2.13	2	0.16
Intercept only + T	3.29	1	0.09
% Sedge and grass cover + T	3.54	2	0.08
% Forb cover + T	4.10	2	0.06
% tall shrubs + T	4.45	2	0.05
% Bare ground + T	4.50	2	0.05
Distance to water + T	5.01	2	0.04

* T, a linear time trend across the breeding season

Table AVII. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and proximity to Mew Gulls (*Larus canus*). Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for godwit nests grouped by plot (North and South) found in 2009 – 2016.

Model	$dAIC_C$	k	Weights
Distance to gull colony + T	0.00	2	0.47
Number of species + T	2.13	2	0.16
Intercept only + T	3.29	1	0.09
% Sedge and grass cover + T	3.54	2	0.08
% Forb cover + T	4.10	2	0.06
% tall shrubs + T	4.45	2	0.05
% Bare ground + T	4.50	2	0.05
Distance to water + T	5.01	2	0.04

* T, a linear time trend across the breeding season

Table AVIII. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and proximity to Mew Gulls (*Larus canus*). Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for godwit nests grouped by year (2009, 2010, 2011, 2014, 2015, 2016).

Model	$dAIC_C$	k	Weights
Distance to gull colony + T	0.00	2	0.47
Number of species + T	2.13	2	0.16
Intercept only + T	3.29	1	0.09
% Sedge and grass cover + T	3.54	2	0.08
% Forb cover + T	4.10	2	0.06
% tall shrubs + T	4.45	2	0.05
% Bare ground + T	4.50	2	0.05
Distance to water + T	5.01	2	0.04

* T, a linear time trend across the breeding season

Table AIX. Summary of competing GLMM models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) chick survival and proximity to Mew Gulls (*Larus canus;* MEGU). Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for godwit nests with random effects of brood and year.

Model	$dAIC_C$	k	Weight
Distance to MEGU colony	0.00	4	0.95
Distance to MEGU nest	6.70	4	0.03
Null	9.90	3	0.01
Distance nest was to MEGU colony	10.90	4	0.00
Distance to closest pond	11.50	4	0.00
Number of MEGU nests	11.50	4	0.00

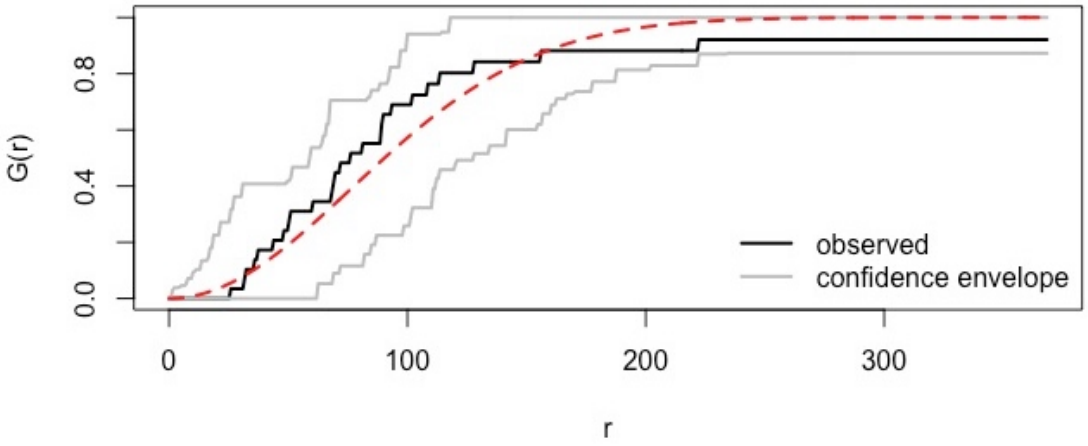


Figure A1. G function for all Hudsonian Godwit (*Limosa haemastica*) and Mew Gull (*Larus canus*) nests found on North plot between 2014 and 2016. The solid black line represents values for the point pattern (observed), dashed red line represent the expectation under complete spatial randomness (theoretical) of the Poisson null model, and the gray lines represent the confidence envelope based on 199 randomizations of a Poisson point process. Values above the upper bounds of the confidence envelope indicate clustering at distance r, and values below the lower bounds indicate inhibition.

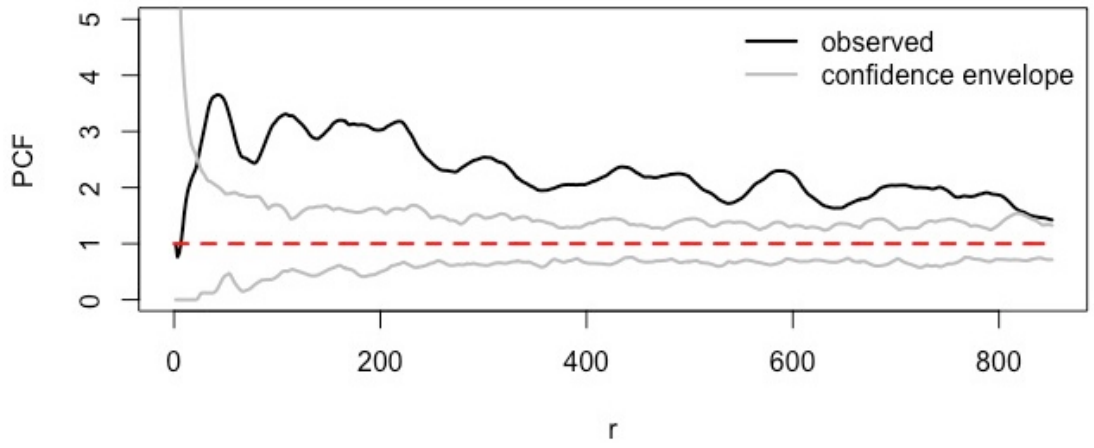


Figure A2. PCF function for all Hudsonian Godwit (*Limosa haemastica*) and Mew Gull (*Larus canus*) nests found on North plot between 2014 and 2016. The solid black line represents values for the point pattern (observed), dashed red line represent the expectation under complete spatial randomness (theoretical) of the Poisson null model, and the gray lines represent the confidence envelope based on 199 randomizations of a Poisson point process. Values above the upper bounds of the confidence envelope indicate clustering at distance r, and values below the lower bounds indicate inhibition.

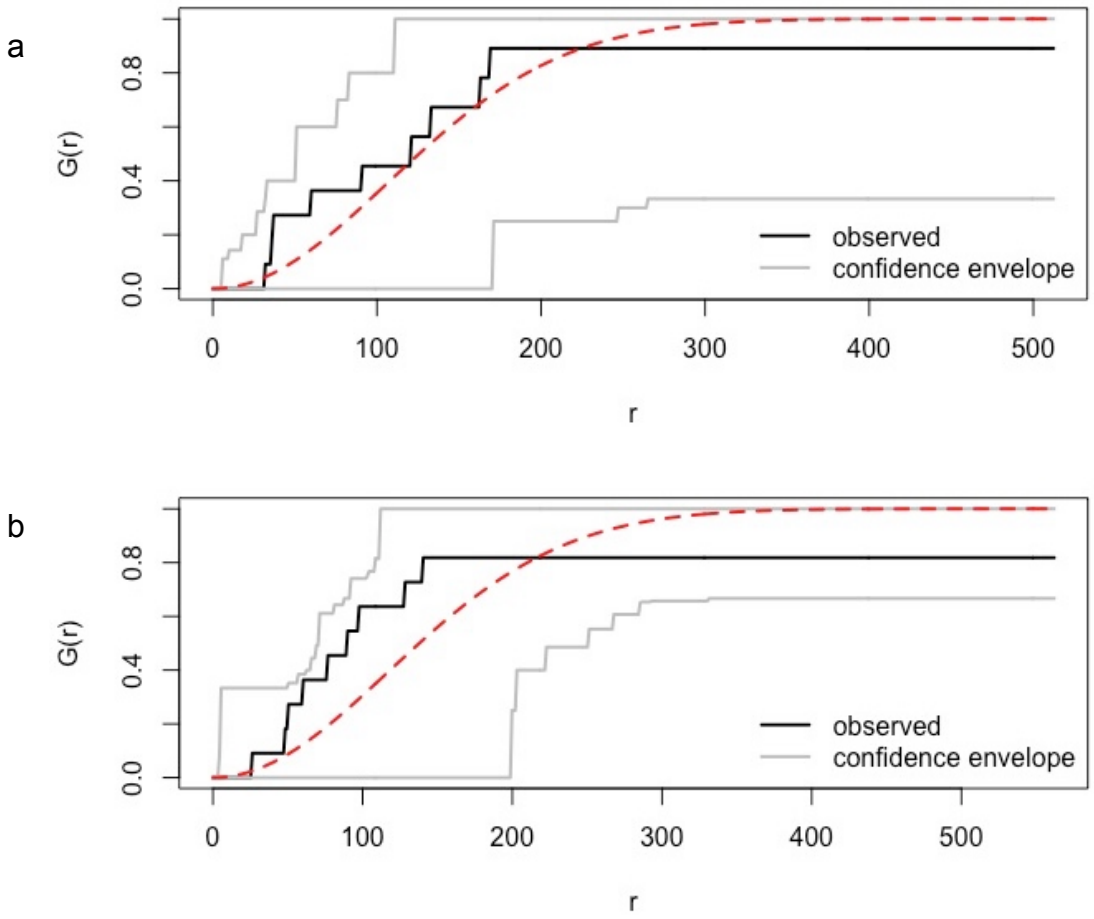


Figure A3. G function for Hudsonian Godwit (*Limosa haemastica*) and Mew Gull (*Larus canus*) nests found on North plot in 2015 (a) and 2016 (b). The solid black line represents values for the point pattern (observed), dashed red line represent the expectation under complete spatial randomness (theoretical) of the Poisson null model, and the gray lines represent the confidence envelope based on 199 randomizations of a Poisson point process. Values above the upper bounds of the confidence envelope indicate clustering at distance r, and values below the lower bounds indicate inhibition.

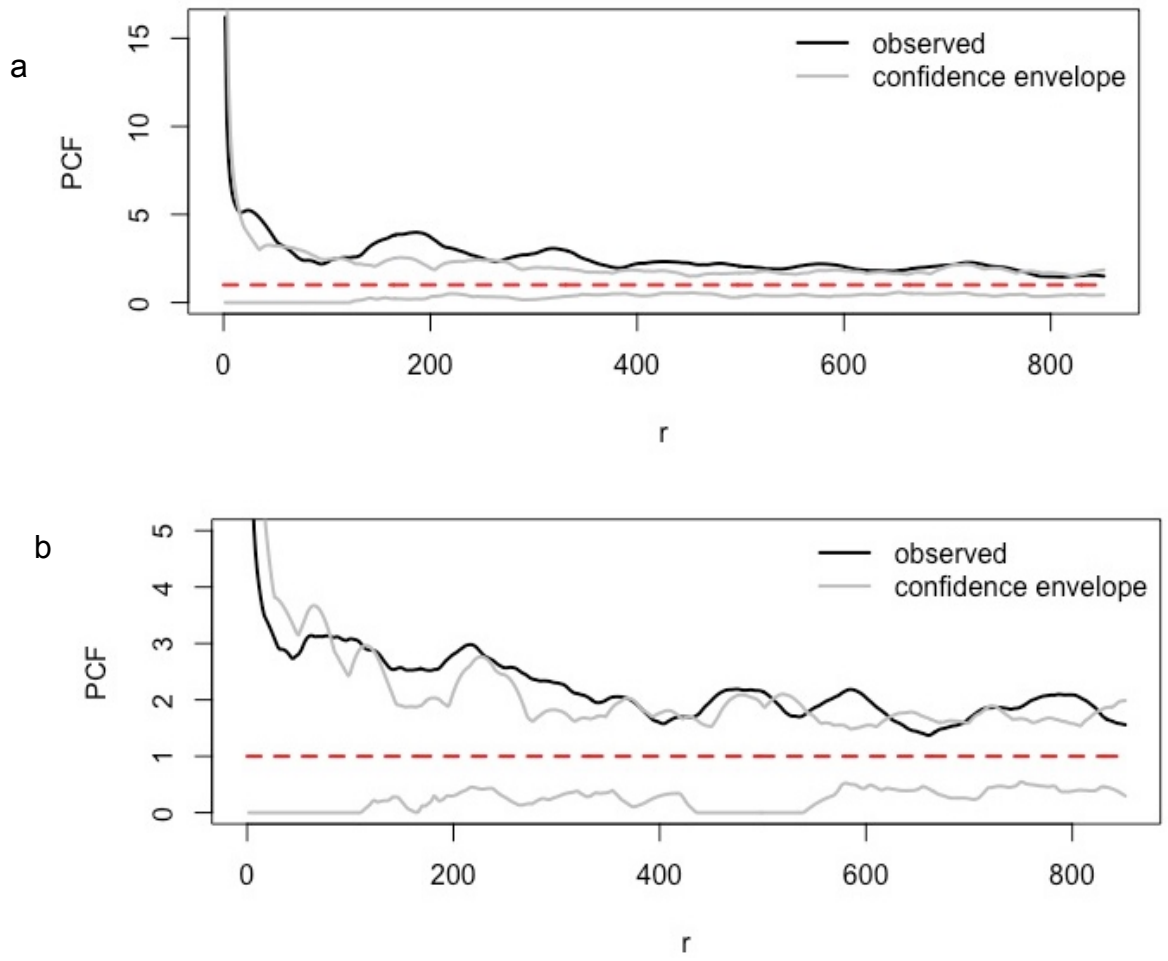
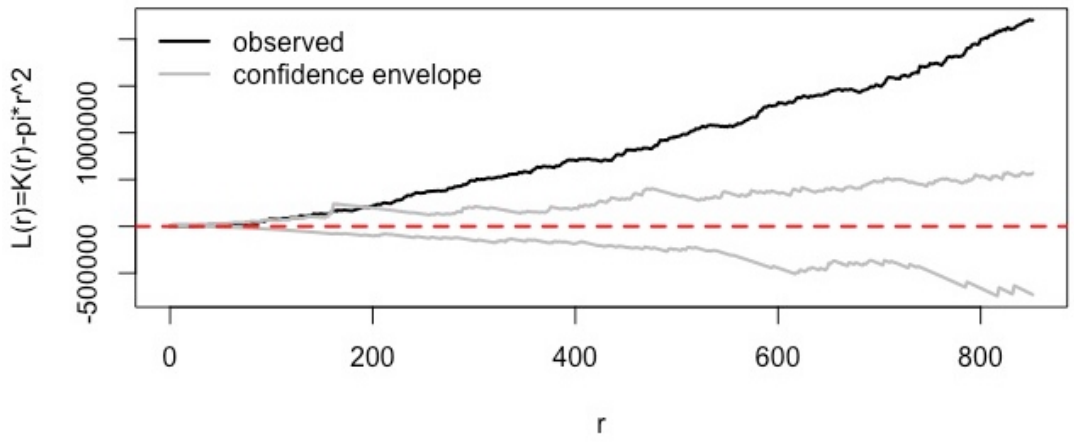


Figure A4. PCF function for Hudsonian Godwit (*Limosa haemastica*) and Mew Gull (*Larus canus*) nests found on North plot in 2015 (a) and 2016 (b). The solid black line represents values for the point pattern (observed), dashed red line represent the expectation under complete spatial randomness (theoretical) of the Poisson null model, and the gray lines represent the confidence envelope based on 199 randomizations of a Poisson point process. Values above the upper bounds of the confidence envelope indicate clustering at distance r, and values below the lower bounds indicate inhibition.

a



b

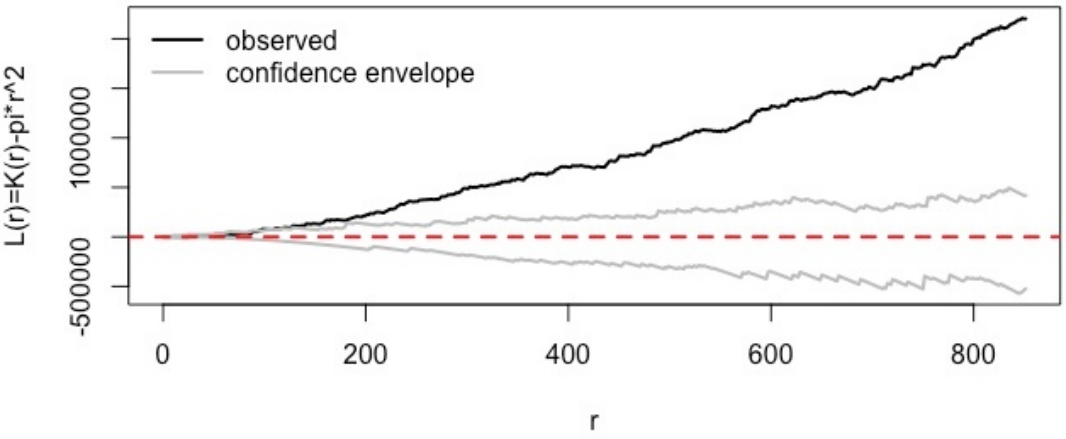


Figure A5. Ripley's K function (transformed to L(r)) for (a) successful Hudsonian Godwit (*Limosa haemastica*) and all Mew Gull (*Larus canus*) nests and (b) failed Hudsonian Godwit and all Mew Gull nests found on North plot in 2016. The solid black line represents values for the point pattern (observed), dashed red line represent the expectation under complete spatial randomness (theoretical) of the Poisson null model, and the gray lines represent the confidence envelope based on 199 randomizations of a Poisson point process. Values above the upper bounds of the confidence envelope indicate clustering at distance r, and values below the lower bounds indicate inhibition.

APPENDIX B

Table BI. Nest survival, nest site microhabitat characteristics, and proximity to Mew Gulls (*Larus canus*) data for all Hudsonian Godwit (*Limosa haemastica*) nests found at Beluga River, Alaska from 2009 to 2016. Distance to the closest gull nest and number of gull nests within 200 m were only collected between 2014 and 2016.

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to gull nest (m)	Number of gull nests	Distance to water (m)	% 30cm to 1m	% Bare	% Sedge Grass	% Forb	Number of species
GN1	10	31	31	Hatch	2009	North	0	NA	NA	5.21	21	13	25	13	14
GN10	6	28	28	Hatch	2009	North	0	NA	NA	10.88	73	5	31	16	12
GN12	10	31	31	Hatch	2009	North	0	NA	NA	0.50	60	2	31	17	15
GN14	10	29	29	Hatch	2009	North	0	NA	NA	17.31	50	0	31	15	14
GN17	8	17	19	Fail	2009	South	62.31	NA	NA	0.36	33	35	19	7	9
GN18	10	12	15	Fail	2009	North	0	NA	NA	16.50	36	0	30	16	18
GN2	6	30	30	Hatch	2009	North	0	NA	NA	3.02	30	30	10	12	13
GN22	11	33	33	Hatch	2009	North	84.24	NA	NA	9.14	57	6	26	24	15
GN27	15	33	33	Hatch	2009	North	0	NA	NA	8.08	43	10	16	15	16
GN28	5	17	19	Fail	2009	South	0	NA	NA	5.59	22	10	23	13	20
GN43	10	17	19	Fail	2009	South	0.89	NA	NA	8.02	55	7	33	17	20
GN44	14	28	28	Hatch	2009	North	0	NA	NA	12.92	40	0	38	16	17
GN45	19	32	32	Hatch	2009	North	450.32	NA	NA	13.72	52	0	28	12	15
GN46	19	33	33	Hatch	2009	North	0	NA	NA	0.30	33	10	32	13	16
GN47	21	27	27	Hatch	2009	North	0	NA	NA	3.69	40	7	23	15	17
GN48	27	29	29	Hatch	2009	North	0	NA	NA	0.50	18	2	30	15	13
GN49	28	33	33	Hatch	2009	North	0	NA	NA	16.31	43	0	30	17	20
GN7	15	33	33	Hatch	2009	North	0	NA	NA	12.80	39	0	34	13	18
GN8	27	28	28	Hatch	2009	North	0	NA	NA	6.68	26	9	31	16	16
GN07	9	9	10	Fail	2010	North	98.14	NA	NA	3.53	0	20	11	9	20
GN11	18	41	41	Hatch	2010	North	0	NA	NA	2.67	4	7	9	10	18
GN41	7	7	8	Fail	2010	North	0	NA	NA	0.50	12	26	12	12	24
GN43	9	9	10	Fail	2010	North	0	NA	NA	30.28	15	1	10	8	17
GN47	10	34	34	Hatch	2010	South	106.36	NA	NA	3.51	2	3	18	8	19
GN49	11	11	13	Fail	2010	North	0	NA	NA	18.21	1	3	13	7	16
GN53	16	33	33	Hatch	2010	South	0	NA	NA	5.03	5	25	18	10	20
GN55	20	20	21	Fail	2010	North	0	NA	NA	1.86	3	4	11	10	20
GN56	22	22	23	Fail	2010	North	194.49	NA	NA	4.52	8	10	13	7	14

TABLE BI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to gull nest (m)	Number of gull nests	Distance to water (m)	% 30cm to 1m	% Bare	% Sedge Grass	% Forb	Number of species
GN57	17	17	19	Fail	2010	North	176.65	NA	NA	4.70	12	25	11	9	18
GN58	23	43	43	Hatch	2010	North	0	NA	NA	18.59	5	2	8	13	25
GN61	30	31	31	Hatch	2010	South	82.99	NA	NA	0.50	4	12	12	8	19
GNHUYU	1	29	29	Hatch	2010	South	87.92	NA	NA	1.93	10	4	14	7	19
GNHX	13	38	38	Hatch	2010	North	0	NA	NA	1.65	4	1	13	15	24
GNHXXC	4	6	9	Fail	2010	North	0	NA	NA	11.07	13	1	10	8	17
GNKX	13	30	30	Hatch	2010	North	0	NA	NA	16.00	15	1	10	12	23
GNPE	7	7	9	Fail	2010	North	0	NA	NA	10.49	1	0	13	11	19
GNPEJA	14	41	41	Hatch	2010	North	0	NA	NA	10.00	8	0	8	7	19
GNPK	20	46	46	Hatch	2010	North	0	NA	NA	12.98	1	6	14	12	23
GNPM	43	44	44	Hatch	2010	North	0	NA	NA	5.06	5	12	16	11	19
GNUL	2	30	30	Hatch	2010	North	0	NA	NA	13.51	3	1	14	6	14
GNXKTV	14	26	27	Fail	2010	North	450.32	NA	NA	10.14	5	2	13	7	17
GNYMXV	29	30	30	Hatch	2010	North	0	NA	NA	17.12	22	1	8	7	19
GNYN	6	6	7	Fail	2010	North	38.20	NA	NA	11.17	2	1	9	8	16
GNYN2	22	46	46	Hatch	2010	North	0	NA	NA	1.60	2	12	41	5	9
GNYTXL	7	27	27	Hatch	2010	South	0	NA	NA	4.19	18	7	33	11	19
GNYV	6	6	7	Fail	2010	North	0	NA	NA	20.32	10	2	19	13	19
GNYV2	14	20	24	Fail	2010	North	0	NA	NA	2.36	8	30	21	9	13
GN08	21	44	44	Hatch	2011	North	0	NA	NA	8.50	15	0	47	7	10
GN10	27	37	37	Hatch	2011	North	0	NA	NA	12.56	1	0	31	8	9
GN12	28	42	44	Fail	2011	North	10.11	NA	NA	7.80	2	0	35	7	6
GN13	35	38	38	Hatch	2011	North	0	NA	NA	6.13	25	0	32	15	12
GNAPAU	34	35	35	Hatch	2011	North	0	NA	NA	7.47	30	0	16	8	8
GNC4MJ	6	33	33	Hatch	2011	North	92.80	NA	NA	8.53	20	2	37	11	10
GNCC	7	14	16	Fail	2011	North	0	NA	NA	16.57	5	0	66	7	10

TABLE BI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to gull nest (m)	Number of gull nests	Distance to water (m)	% 30cm to 1m	% Bare	% Sedge Grass	% Forb	Number of species
GNCT	32	33	33	Hatch	2011	North	0	NA	NA	0.21	20	25	6	7	12
GNE5E9	26	41	41	Hatch	2011	North	0	NA	NA	1.16	5	0	54	10	4
GNEAE7	6	32	32	Hatch	2011	North	0	NA	NA	9.75	35	5	11	37	10
GNH7T2	19	40	40	Hatch	2011	North	0	NA	NA	7.62	70	0	31	14	13
GNH8L0	8	29	29	Hatch	2011	South	0	NA	NA	8.6	20	0	49	8	10
GNJMXH	13	17	19	Fail	2011	South	31.13	NA	NA	4.66	65	5	46	9	10
GNJTMU	37	38	38	Hatch	2011	North	444.42	NA	NA	9.63	30	1	48	11	12
GNK0PM	20	31	31	Hatch	2011	North	0	NA	NA	13.17	60	3	45	10	9
GNK4T7	15	31	31	Hatch	2011	South	232.07	NA	NA	25.82	40	4	41	7	6
GNK5L4	27	34	35	Fail	2011	North	69.03	NA	NA	11.58	30	5	22	17	8
GNL5E6	20	31	33	Fail	2011	South	23.67	NA	NA	24.94	65	5	43	6	8
GNM2P2	14	31	31	Hatch	2011	North	0	NA	NA	8.02	20	12	44	17	5
GNM3U0	19	35	35	Hatch	2011	North	0	NA	NA	16.67	4	0	28	17	14
GNN8X3	7	34	34	Hatch	2011	North	0	NA	NA	8.08	20	5	55	9	12
GNTANA	30	31	31	Hatch	2011	North	0	NA	NA	7.74	70	5	24	14	12
GNV9C0	22	37	37	Hatch	2011	North	0	NA	NA	16.28	10	0	24	7	8
GNX50H	8	30	30	Hatch	2011	North	0	NA	NA	6.71	75	0	30	13	13
GNX6H3	6	29	29	Hatch	2011	North	0	NA	NA	5.43	10	0	47	9	10
GNXA	12	12	14	Fail	2011	North	127.49	NA	NA	3.66	60	0	53	11	11
GNY0T4	13	22	24	Fail	2011	South	0	NA	NA	29.26	55	2	43	16	12
GNY9L6	14	34	34	Hatch	2011	North	0	NA	NA	12.01	20	5	18	19	15
BHD11	20	32	32	Hatch	2014	South	0	89.56	2	1.30	0	0	35	15	5
BHD17	33	47	47	Hatch	2014	South	0	107.06	1	0.25	0	75	14	2	3
BHD19	38	43	43	Hatch	2014	North	0	50.63	6	14.40	3	0	23	6	7
BJL17	14	31	31	Hatch	2014	North	155.91	343.99	0	3.50	8	0	30	8	7
BJL18	18	39	39	Hatch	2014	North	0	326.84	0	0.50	3	10	30	4	8

TABLE BI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to gull nest (m)	Number of gull nests	Distance to water (m)	% 30cm to 1m	% Bare	% Sedge Grass	% Forb	Number of species
BJL19	22	34	34	Hatch	2014	North	0	89.29	7	7.50	3	0	37	7	5
BJL23	30	31	31	Hatch	2014	North	1	240.74	0	11.25	5	0	10	13	8
BJL25	31	32	32	Hatch	2014	South	0	179.79	1	5.25	3	0	60	8	5
GJM06	16	35	35	Hatch	2014	South	61.82	99.48	4	0.25	15	20	31	11	7
GJM17	37	38	38	Hatch	2014	North	0	114.23	2	7.75	0	0	30	12	7
RJS27	35	35	37	Fail	2014	North	0	52.07	3	9.25	2	0	51	13	10
GJM05	8	31	31	Hatch	2015	North	0	168.67	4	8.25	30	0	53	7	6
GJM18	12	32	32	Hatch	2015	South	95.72	122.12	6	0.50	30	2	36	4	8
GJM35	16	31	31	Hatch	2015	North	0	132.57	2	25.5	15	0	34	10	8
GJM36	17	40	40	Hatch	2015	South	0	74.03	16	0.65	0	0	43	12	9
GJM56	23	30	30	Hatch	2015	North	0	35.88	9	13.60	30	0	31	14	11
JAK05	9	34	34	Hatch	2015	North	0	31.49	15	9.98	45	0	26	8	6
JAK21	13	34	34	Hatch	2015	North	0	36.79	5	1.45	40	0	25	7	6
JMH10	12	37	37	Hatch	2015	South	35.74	136.30	4	28.30	20	0	30	9	6
JMH120	37	38	38	Hatch	2015	South	83.54	126.89	3	12.50	10	0	31	9	5
JMH15	14	14	15	Fail	2015	North	352.56	414.19	0	7.75	5	0	41	13	11
JMH20	16	34	34	Hatch	2015	North	0	60.05	7	16.30	40	0	28	9	7
JMH28	20	32	32	Hatch	2015	North	47.46	162.91	1	7.25	40	0	25	15	11
KJP11	11	31	31	Hatch	2015	North	0	112.06	4	13.50	60	0	25	44	15
KJP18	12	31	31	Hatch	2015	South	0	65.62	5	8.00	15	0	55	9	5
KJP44	20	32	32	Hatch	2015	North	0	91.03	10	55.30	30	0	17	8	12
RJS05	27	40	40	Hatch	2015	North	0	120.49	7	8.40	20	0	36	9	8
KRS48	23	29	29	Hatch	2016	North	0	50.38	5	18.25	60	0	32	3	8
KRS63	29	29	30	Fail	2016	North	397.62	482.11	0	0.99	10	0	20	15	10
LKF04	8	31	31	Hatch	2016	South	4.28	92.35	3	4.25	12	0	38	12	12
LKF15	14	31	32	Fail	2016	North	0	140.29	4	21.3	50	0	9	11	8

TABLE BI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to gull nest (m)	Number of gull nests	Distance to water (m)	% 30cm to 1m	% Bare	% Sedge Grass	% Forb	Number of species
LKF22	19	37	37	Hatch	2016	South	181.24	182.20	1	27.50	0	0	66	9	10
LKF23	20	27	29	Fail	2016	North	4.88	76.03	4	7.65	20	0	33	7	7
MLS14	11	29	29	Hatch	2016	North	0	60.35	3	16.25	25	0	17	12	10
MLS37	19	37	37	Hatch	2016	South	295.37	386.06	0	4.30	8	0	36	9	8
RIG01	9	9	11	Fail	2016	North	105.40	127.82	1	5.50	8	0	31	5	10
RIG15	21	42	42	Hatch	2016	North	0	96.98	10	3.45	5	0	37	3	6
RJS01	6	9	12	Fail	2016	North	152.07	347.93	0	4.85	30	0	38	8	11
RJS02	9	15	18	Fail	2016	North	0	47.81	5	5.30	8	0	21	14	13
RJS04	12	32	32	Hatch	2016	North	0	89.39	5	38.50	35	0	13	7	10
RJS07	15	32	32	Hatch	2016	North	0	25.63	7	4.00	2	0	21	20	16
RJS10	17	32	32	Hatch	2016	South	211.02	240.26	0	20.50	18	0	14	9	13
RJS16	31	34	34	Hatch	2016	South	210.32	245.94	0	28.60	15	0	10	12	10

Table BII. Hudsonian Godwit (*Limosa haemastica*) chick survival to five-days-old and proximity to Mew Gull (*Larus canus*) data in Beluga River, Alaska from 2014 to 2016.

Chick	Brood	Year	Chick Fate	Distance to gull colony (m)	Distance to gull nest (m)	Number of gull nests	Distance to pond (m)	Nest's distance to gull colony (m)
H03	2014HUGOBHD17	2014	Died	0	78.07	1	56.10	0
J81	2014HUGOBJL17	2014	Survived	479.25	626.40	0	4.46	155.91
1AV	2014HUGOBJL18	2014	Died	0	169.19	1	1.85	0
H30	2014HUGOBJL19	2014	Died	0	107.25	8	29.88	0
1EP	2014HUGOBJL25	2014	Survived	157.63	383.23	0	71.29	0
C23	2014HUGOGJM06	2014	Survived	65.45	225.34	0	9.28	61.82
J03	2015HUGOFUV	2015	Died	0	293.75	0	5.26	NA
1KU	2015HUGOGJM18	2015	Died	148.36	172.55	5	27.47	95.72
E85	2015HUGOGJM35	2015	Survived	207.80	236.93	0	0	0
E53	2015HUGOJAK05	2015	Survived	0	125.63	7	20.32	0
1KJ	2015HUGOJAK21	2015	Survived	0	212.36	0	16.71	0
A83	2015HUGOJMH10	2015	Survived	191.29	227.43	0	11.17	35.74
H66	2015HUGOJMH28	2015	Died	0	114.03	2	18.22	47.46
H64	2015HUGOKJP18	2015	Survived	0	109.78	4	47.03	0
H96	2015HUGOKJP44	2015	Died	123.11	294.68	0	2.86	0
1LU	2015HUGORJS05	2015	Died	25.75	192.88	1	37.94	0
1KK	2016HUGOKRS48	2016	Died	0	68.20	6	7.99	0
1TU	2016HUGOLKF04	2016	Survived	0	60.35	3	4.83	4.28
1KA	2016HUGOLKF22	2016	Died	0	13.62	9	0	181.24
1CM	2016HUGOMLS14	2016	Died	0	35.44	5	8.46	0
C77	2016HUGOMLS37	2016	Died	0	43.12	19	3.55	295.37
1HH	2016HUGORIG15	2016	Died	0	70.16	8	0	0
H75	2016HUGORIG15	2016	Died	0	100.93	8	5.03	0
1LT	2016HUGORJS07	2016	Survived	0	116.02	8	30.22	0
H84	2016HUGORJS07	2016	Survived	0	100.95	8	30.58	0
1KV	2016HUGORJS10	2016	Survived	0	38.75	16	21.02	211.02
H11	2016HUGORJS10	2016	Survived	0	45.31	15	30.20	211.02
1MU	2016HUGORJS16	2016	Survived	146.10	198.77	1	21.91	210.32
C97	2016HUGORJS16	2016	Survived	152.36	204.26	0	11.44	210.32

CHAPTER THREE

NEST SURVIVAL WITHIN AND OUTSIDE OF A PROTECTIVE NESTING ASSOCIATION

Abstract:

A wide range of reproductive behaviors – including nest site selection, reproductive phenology, and defensive behaviors – can reflect selective pressures to reduce the risk of nest predation. However, such behaviors do not operate in isolation, and the interactions and feedbacks among them remain poorly understood. In this study, we tested the extent to which a protective nesting association mediated how nest site characteristics or individual traits of breeding Hudsonian Godwits (*Limosa haemastica*) influenced nest survival. From 2009 – 2016 at Beluga River, Alaska, we monitored 141 godwit nests located within and outside of breeding colonies of Mew Gulls (*Larus canus*), which aggressively defend their nests from predators and, thereby, may reduce predation risk for godwit nests located within their colonies. We examined how the characteristics of individuals and the drivers of nest survival may vary within and outside of Mew Gull colonies. Consistent with reduced predation risk, males were less often present at the nest during the day and gave fewer alarm calls within than outside of gull colonies, and females were also larger within gull colonies. Nest survival was best explained by a combination of individual attributes and nest site characteristics, though relationships differed within and outside of colonies. Specifically, survival of godwit nests outside of – but not within – colonies improved with male body condition, and survival within colonies improved with female body condition. Our study, thus, provides evidence that godwits nesting in association with Mew Gull colonies exhibit different drivers of nest survival within and outside of gull colonies.

Keywords: protective nesting association, nest survival, individual quality, body condition, shorebird, microhabitat

Introduction:

Nest predation is one of the most common causes of reproductive failure in birds and, thus, is expected to be an important evolutionary driver shaping nest site selection and behavior (Ricklefs 1969, Martin 1993). Adaptive behaviors to reduce nest loss by predation depend on a variety of ecological factors, including the environmental attributes of the nest site, as well as the behaviors of potential nest predators (Martin 1995, Martin et al. 2000, Jedlikowski and Brambilla 2017). Birds employ several strategies to avoid predation, including egg or plumage crypsis and the placement of nests in locations that are inaccessible to predators (e.g., islands or cliffs; Nguyen et al. 2003, McKinnon et al. 2010, Iverson 2014). Although high densities of nesting birds may attract predators in certain contexts, dense colonies can also provide protection. Individuals in synchronously breeding colonies are thought to benefit from predator swamping and improved detection of – and defense from – predators (Wiklund 1982, Wittenberger and Hunt 1985, Richardson and Bolen 1999). Another strategy that may be used to reduce predation risk is to nest within heterospecific aggregations known as "protective nesting associations", that improve reproductive performance of at least one of the species (Burger 1984, Quinn and Ueta 2008). In protective associations, an associate species benefits from aggressive nest defense by a protector species or from information gleaned from the protector species about the whereabouts of predators (Nuechterlein 1981, Quinn and Ueta 2008). Protective associations can thus reduce an individual's risk of nest predation through community-level interactions.

Aggressive or defensive behaviors of protector species can dissuade individual predators from using particular areas and even affect entire predator communities. Nonetheless, protector species can also vary in both their effectiveness and reliability at deterring or excluding predators (Larsen and Grundetjern 1997, Quinn et al. 2003). For instance, the presence of predators, such

as owls and raptors, can alter both species composition and abundance of other predators near their nests. “Predator-exclusion zones” have been documented in the vicinity of breeding Snowy Owls (*Nyctea scandiaca*) and are associated with improved nest survival of the protected species (Bêty et al. 2001, van Kleef et al. 2007, Kharitonov et al. 2013). Even in cases where less aggressive protectors cannot exclude specific predators (Stenhouse et al. 2005), protected species may still benefit from a less complex or abundant predator community. However, the complexity of inter-specific interactions ultimately makes it difficult to generalize about the nature and extent of benefits derived from protective associations. For instance, Spotted Sandpipers (*Actitis macularia*) nest within Common Tern (*Sterna hirundo*) colonies for protection from minks (*Mustela vison*), but still experience high egg predation by Ruddy Turnstones (*Arenaria interpres;* Alberico et al. 1991). Thus, protective associations create complex heterogeneity in predation risk.

Because protective associations lessen the risk of predation, they may alter selective pressures on nest survival more generally, especially as related to anti-predator behaviors, nest site characteristics, and the quality of the individuals nesting within an area (Smith et al. 2007). For example, Red Phalaropes (*Phalaropus fulicarius*) nesting within Sabine’s Gull (*Xema sabini*) colonies flush at greater distances in response to approaching predators and take more frequent and extended incubation recesses. By adjusting their anti-predator behaviors within the colony, individuals can minimize predation risk to both the nest and themselves (Smith et al. 2007). Individuals may also select for different nest site characteristics (e.g., concealment) within and outside of a nesting association (Smith et al. 2007). Lastly, higher quality individuals – in terms of age, experience, or physical condition – are likely to occupy better quality nest sites or obtain better quality mates (Lifjeld and Slagsvold 1988, Kim and Monaghan 2005, Johnson and Walters

2011), and may settle within protective associations to the exclusion of lower quality individuals. The predictable spatio-temporal variation in predation risk created by a protective association can thus alter the individual attributes and behaviors that influence nest survival.

Our understanding of how nest site characteristics and individual attributes affect nest survival within and outside of a protective nesting association is limited. In this study, we focus on Hudsonian Godwits (*Limosa haemastica*; hereafter 'godwits') breeding in the sub-arctic, where they form stable non-habitat-based aggregations with Mew Gulls (*Larus canus*; hereafter 'gulls'), which act as a protector species (Swift et al. 2017a, Swift et al. 2018). However, there is an important trade-off – whereas godwit nests within colonies are more likely to successfully hatch, the chicks hatched from those nests are more likely to be depredated by gulls (Swift et al. 2018). Godwits may therefore choose different nest locations across the landscape with regard to gull colonies to maximize either their nest or chick survival. Or, alternatively, they may adopt a strategy that increases both nest and chick survival through differences in behavior depending on the stage of the breeding season and their location relative to the gull colony.

We investigated whether the characteristics of individual godwits, as well as the drivers of nest survival, differed within and outside of gull colonies. We hypothesized that for godwits nesting within gull colonies, selection pressure on nest survival may be relaxed due to the protection received from the nesting association. Specifically, we examined how individual body condition, microhabitat of nests, and defensive behaviors differed between birds nesting within and outside of colonies and the extent to which these factors influenced nest survival was context-dependent. Although accounts of heterospecific nesting colonies are relatively common in birds, few studies have compared drivers of nest survival of colonial and non-colonial individuals in the same area and year. Our study thus provides a unique perspective on the

influence of a protective nesting association on the drivers of nest survival of the protected species.

Methods:

Study area and species:

We studied a population of Hudsonian Godwits breeding in Beluga River, Alaska (61.21°N, 151.03°W), within a study area of ~8 km^2 from 2009 – 2012 and 2014 – 2016. The study area was divided into two study plots of uninterrupted muskeg bog of unequal sizes – North (550 ha) and South (120 ha) – that were separated by ~7 km of unmonitored boreal forest and muskeg bog.

Godwits are monogamous with biparental care, where both the male and female defend the territory and incubate the nest. Adults divide incubation duties with females typically incubating during the day and males at night (Walker et al. 2011, Bulla et al. 2016). Godwits breed in open bogs, tundra, and fens dominated by sedges, *Carex* spp., and dwarf birch, *Betula glandulosa/nana* (Swift et al. 2017a). In Beluga River, the main predators of godwit nests include red foxes (*Vulpes vulpes*), Common Ravens (*Corvus corax*), and Sandhill Cranes (*Grus canadensis*). Adult godwits are also vulnerable to predation by Northern Harriers (*Circus cyaneus*) while incubating. Our previous work showed that habitat heterogeneity did not explain spatial aggregations of godwit nests (Swift et al. 2017b), but, instead, the presence of Mew Gull colonies did (Swift et al. 2018). Godwits nesting within a gull colony have increased nest survival compared with godwits nesting at increasing distances from a gull colony or with fewer numbers of nearby nesting gulls, thereby benefiting from a protective nesting association during incubation (Swift et al. 2018).

Nest distribution and fate:

We systematically searched plots for nests every two-to-three days throughout the nesting season (May–July). We searched for nests (scrape containing ≥ one egg) using a combination of prior knowledge, systematic searching, and behavioral observations. Upon discovery of a nest, we recorded a GPS location and floated eggs to estimate the timing of nest initiation, and hence, the age of the nest (Liebezeit et al. 2007). We did not physically mark nest locations to minimize the chance of associative learning by predator species (Reynolds 1985). We revisited nests every two-to-three days until either one day prior to the expected hatch or until we observed starred or pipped eggs. We typically checked nests by resighting incubating birds with binoculars from 20-30 m away. Adults were flushed weekly (at most) to minimize disturbances that might increase the probability of nest failure, and field teams did not approach nests directly when predators were observed nearby. A nest was considered successful if ≥1 egg hatched and chicks successfully left the nest site. Nest failure was presumed when we found empty nests early in the incubation period or destroyed eggs. Due to low rates of nest abandonment in this system (Senner et al. 2017), we considered the failure rate of nests in our study to represent the depredation rate as well.

Habitat metrics:

We measured the habitat at each nest site after the nest was no longer active. We defined the nest site as the area within a 1 m diameter circle centered on the nest. For each nest, we measured the distance to the nearest water body (≥ 2 cm deep) from the center of the circle, and, within the circle itself, the percent cover of all plant species present. We summarized the percentage of the circle covered by shrubs between 30 cm and 1 m tall as well as the percentage

of sedges, grasses, and forbs (see Swift et al. 2017a, b for more information). We also described the percent of the nest concealed by vegetation from 1 m directly above the nest scrape.

Godwit body condition:

Incubating individuals were captured using a mist net (n = 231) and marked with a U.S. Geological Survey metal band, a year-specific color band, and a uniquely coded alpha-numeric flag. For each individual, we measured its tarsus length (to a precision of 0.1 mm) and body mass (to 0.1 g). An individual's size-adjusted mass (hereafter termed "condition") was then calculated using the residuals of a regression between mass and tarsus. Because tarsus and size-adjusted mass were positively correlated (r = 0.63), we use the term "larger" to refer to greater size-adjusted mass throughout the manuscript. Measurements of mass were adjusted for the day of incubation because mass declines steadily in both males (-0.48, 95% CI -0.91, -0.05; p-value = 0.03) and females (-0.54, 95% CI -1.05, -0.02; p-value = 0.04) during the incubation period and captures occurred throughout incubation (mean: day 13; range: day 3 – 27). Only one individual from the breeding pair was captured for 14 nests, and neither individual was captured for 32 nests.

Godwit defensive behaviors:

For each godwit nest found in 2015 and 2016, we recorded the defensive behaviors exhibited by the parents during mid-incubation (day 11 – 13). Typically, two observers used a 2 – 5 minute observation period during which they recorded the number of calls and flights made by the individual(s) present at the nest. At the beginning of the observation period, one observer approached the nest and flushed the incubating adult while the other maintained a distance of 20-

30 m and recorded the ensuing period with an audio recording unit. Audio recordings were then transcribed using CowLog (Pastell 2016), and we calculated the number of calls and flights per minute from the transcription. Additionally, the minimum distance that an individual godwit approached the observer at the nest was recorded for each godwit present.

Godwit nest survival analyses:

We examined the influence of habitat characteristics and body condition on godwit nest survival with mark-recapture analyses (Table I). Using all gull nests found from 2014 – 2016, we created a minimum convex polygon for each plot that we defined as the gull colony (see Swift et al. 2018 for more information). For each godwit nest, we calculated the minimum distance to the gull colony boundary using ArcGIS (ESRI 2015), and any nest within 25 m of this boundary was considered effectively within the gull colony. We also selected habitat variables known to be used by godwits when choosing their nest sites (Swift et al. 2017a): distance to the closest water body (≥ 2 cm deep), percent tall shrubby cover (between 30 cm and 1 m tall), percent sedge, grass, and herbaceous forb cover, and percent overhead nest cover. Lastly, we included our adjusted measure of individual body condition for both members of the breeding pair.

We used generalized linear mixed models (GLMM) with a random effect of 'plot' and a binomial link to test for significant differences between nests within and outside of gull colonies in program R (R Core Development Team 2017). Additionally, we compared the defensive behaviors of godwits nesting within or outside of gull colonies using a separate GLMM analysis. The significance of each model was assessed using a Bonferroni correction to account for non-independence among multiple tests.

We examined the effects of habitat characteristics and body condition on daily nest survival rates (DSR) using the nest-survival method in Program MARK (v. 8.2; White and Burnham 1999) for 141 nests monitored from 2009 – 2012 and 2014 – 2016 using parallel, separate analyses for nests found within (n = 103) and outside (n = 38) of gull colonies (Dinsmore et al. 2002, Rotella et al. 2004). Because our sample sizes were limited, especially outside of gull colonies, we could not perform a single comprehensive analysis and, instead, ran two separate analyses. Following Dinsmore et al. (2002), we compiled an encounter history for each nest by calculating its age when found, age when last known to be active, and age when last checked (i.e., age at hatch for successful nests). We incorporated covariates specific to individual nests and standardized them using the z transformation built into Program MARK (Dinsmore et al. 2002). We linked the response and explanatory variables of the linear model using the logit transformation; this forced parameter estimates to fall within the interval (0, 1) and encouraged model convergence (Dinsmore et al. 2002). Although they were not relevant to our hypotheses, we included both study plot and a linear time trend as covariates in all models as we predicted that differences between study plots and differences in nest age may be important for explaining variation in nest survival. We examined the null model, each variable individually, and all possible combinations between the variable sets both for nests within gull colonies and those outside of gull colonies (20 models; Table I). We ranked models using Akaike's information criterion corrected for small sample size (AIC_C) and selected the most parsimonious model(s) based on AIC_C scores and model weights (w_i; Burnham and Anderson 2002). We plotted and interpreted covariates for which the 95% confidence intervals (CI) of the β estimate did not overlap zero.

Results:

Between 2009 – 2012 and 2014 – 2016, 103 godwit nests were found inside or within 25 m of gull colonies and 38 outside of gull colonies. Daily nest survival was high each year (>96%), but, generally, nest success was 27% higher within gull colonies. Overall, neither nest site microhabitat attributes nor body condition of godwits differed within or outside of gull colonies (Wilk's $\lambda = 0.97$, $p = 0.92$; Table II). However, females were larger within gull colonies (Table II). Defensive behaviors of individuals nesting within and outside of gull colonies were marginally different (Wilk's $\lambda = 0.37$, $p = 0.06$): male godwits that nested outside of gull colonies called more times per minute than males within gull colonies and were present more often during diurnal nest visits (Table III). Due to small sample sizes ($n = 32$), especially outside of gull colonies ($n = 12$), we did not test the defensive behavior variables on nest DSR.

For nests located within gull colonies, four competing models – each including female size-adjusted mass – best explained godwit nest DSR (Table IV). Nest survival most strongly improved with female condition ($\beta = 0.10$, 95% CI 0.02, 0.17; Figure 1), but also marginally increased with cover of tall shrubs between 30 cm and 1 m tall ($\beta = 0.02$, 95% CI -0.01, 0.05), herbaceous cover ($\beta = 0.41$, 95% CI -0.04, 0.85), and declining overhead nest cover ($\beta = -0.31$, 95% CI -0.62, 0.01).

Outside of gull colonies, three competing models – each containing male size-adjusted mass – best explained godwit nest DSR (Table V). Nest survival improved with male condition ($\beta = 0.15$, 95% CI 0.02, 0.28; Figure 2) and was marginally explained by overhead cover ($\beta = 0.06$, 95% CI -0.01, 0.13) and female condition ($\beta = -0.18$, 95% CI -0.87, 0.5).

Discussion:

Protective nesting associations created spatial variation in predation risk and altered drivers of nest success across the landscape in Beluga River, Alaska. Consistent with our previous work, habitat attributes surrounding nests were weak predictors of nest survival and did not differ inside and outside of colonies (Swift et al. 2017a, b, Swift et al. 2018). However, as expected, relationships between nest survival and individual traits differed when godwits associated with a protector species. Within colonies, female godwits were larger, male godwits were less often present at nests, and male godwits sounded fewer alarm calls than those nesting outside of colonies, which is consistent with reduced predation risk. Furthermore, some of these traits affected nest survival, with survival improving with the size-adjusted mass of the parents. However, this was only the case for males outside of colonies and females within colonies. In combination, our results suggest that the predictable spatio-temporal variation in predation risk created by a protective association can alter the drivers of nest survival for individuals.

The lower rates of alarm calls and nest attendance by colony-nesting males were consistent with relaxed selective pressures within colonies due to the protective association with gulls. Other studies show that males with nests in high-risk areas must attend to their territories more often and vocalize more frequently to avoid depredation (Montgomerie and Weatherhead 1988, Martin 1992). Not only do gulls potentially dissuade predators from entering the colony, but also their vocalizations can communicate information about the presence and location of predators (Leger and Nelson 1982, Soard and Ritchison 2009, Shah et al. 2015). Accordingly, we found that males within colonies attended to their nests less during the daytime and called less frequently than did males outside of colonies. The strong positive association between male condition and nest survival outside of colonies is consistent with the idea that larger males are

more effective at protecting nests at night, when males typically incubate, because they require fewer incubation breaks (Montgomerie and Weatherhead 1988, Kleindorfer and Hoi 1997). Thus, outside of colonies alternate individual traits and behaviors appear to drive nest success as compared to within colonies, potentially creating alternate reproductive strategies based on an individual's condition and size-adjusted mass.

We also found that godwit females were larger within gull colonies, a pattern that could be attributed to several factors that are not mutually exclusive. For instance, the fact that females were larger inside the colony might reflect the fact that the colony provided higher quality nesting habitat and was possibly selected by the highest-quality females (Quinn and Ueta 2008). Or, alternatively, because the optimal body mass for a species should reflect a trade-off between the risks of starvation and predation (Lima 1986, Houston et al. 1993, Gosler et al. 1995), female godwits within colonies may be able to adaptively carry more mass without affecting their own survival. In support of this latter hypothesis, our study provides some evidence that the benefits of the "safe" zone extended beyond nest survival and included higher survival of incubating adults. Indeed, the only three adult mortality events we detected in seven years involved incubating females nesting outside of gull colonies. Irrespective of the cause, the larger size of females within colonies may promote nest survival if larger females better defend nests or chicks from predators (Larsen et al. 1996). Relaxed selection pressures within colonies may therefore allow individuals to maximize both nest and adult survival.

In this context and in light of previously documented trade-offs between nest and chick survival across the breeding season (Swift et al. 2018), we suggest that female godwits adopt a bet-hedging approach, whereby they use reproductive strategies most appropriate for their individual body condition. The term "bet-hedging" can be used to refer to three different

strategies: (1) conservative bet-hedging, where individuals "play it safe" by adopting a less variable though less productive strategy; (2) diversified bet-hedging, which spreads risk and minimizes variance in long-term success; and (3) adaptive coin-flipping, where the strategy is selected each year based on the environment (Olofsson et al. 2009, Rees et al. 2010, Chalfoun and Schmidt 2012). These strategies need not be static, and individuals might assess risk and adjust reproductive strategies multiple times across the breeding cycle (Fontaine and Martin 2006, Chalfoun and Martin 2010). Predation risk in our study area was marked by substantial heterogeneity, in part because gulls are an important and spatially-constrained (i.e., to areas near nests) predator of godwit chicks. In our case, the 27% improvement in survival of colony nests was offset by the 28% lower chick survival within colonies (Swift et al. 2018). Conservative bet-hedging in our system may, therefore, occur if larger females opt to maximize adult and nest survival by nesting within gull colonies, despite the comparably greater risks during brood rearing. Females in better body condition may mitigate this risk if they more effectively deter predators and defend broods due to their large size (Hamer and Furness 1993) or can better move broods to safe areas. Alternatively, poor quality females may utilize a diversified bet-hedging approach if they are comparably more effective at defending nests than broods. In this way, individuals in poor condition could take advantage of higher chick survival outside of gull colonies despite the increased variance in nest survival. Ultimately, godwits may be able to improve their fitness by using strategies adjusted for predictable spatio-temporal patterns of risk across different stages of the breeding cycle.

Hudsonian Godwits nesting in association with Mew Gull colonies thus exhibit different drivers of nest survival within and outside of gull colonies. Based on these findings, we suggest that godwits may place nests in the landscape to maximize nest, adult, and chick survival based

on individual size and relative body condition. Our study is among the first to examine the effects of protective associations on the drivers of nest survival, as well as potential differences between individuals choosing to nest within or outside of a protective association. More broadly, our findings suggest that within a heterospecific association, the drivers of nest selection and survival are complex, and further study is needed to disentangle the roles of both biotic and abiotic factors on nest survival.

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TABLES AND FIGURES

Table I. Model suites, variable names, and descriptions of potential variables affecting daily nest survival of Hudsonian Godwits (*Limosa haemastica*) at Beluga River, Alaska during 2009 – 2012 and 2014 – 2016. The defensive behaviors were only collected in 2015 and 2016 and were not included in the MARK models.

Suite	Variable name	Variable description
BODY	Male size-adjusted mass	Residuals from mass, tarsus regression corrected for day of incubation
CONDITION	Female size-adjusted mass	Residuals from mass, tarsus regression corrected for day of incubation
HABITAT	Distance to water (m)	Distance to the closest body of water ≥ 2 cm deep
	% 30 cm<x<1 m	Percent of 1 m diameter circle-plot at the nest that was between 30 cm and 1 m tall; generally tall woody shrubs
	% Sedges, Grasses, Forbs	Percent of 1 m diameter circle-plot comprised of sedge, grass, and forb species
	% Nest cover	Percent of nest concealed from 1 m directly overhead
BEHAVIORS	Male present	Percentage of diurnal nest visits where the breeder male was present on territory
	Female present	Percentage of diurnal nest visits where the breeder female was present on territory
	Male approach distance	Minimum distance the breeder male would approach the observer
	Female approach distance	Minimum distance the breeder female would approach the observer
	Male calls	Number of calls per minute by the breeder male
	Female calls	Number of calls per minute by the breeder female
	Male flights	Number of flights per minute by the breeder male
	Female flights	Number of flights per minute by the breeder female

Table II. Mean and standard error (SE) of Hudsonian Godwit (*Limosa haemastica*) habitat characteristics and body condition within and outside of Mew Gull (*Larus canus*) colonies at Beluga River, Alaska. Percent cover types were estimated within 1 m diameter circle-plots. β coefficients, 95% confidence intervals (CI), and p-values are derived from GLMM analysis.

	Within (n=103)		Outside (n=38)		β	(95% CI)	p-value
	Mean	SE	Mean	SE			
Distance to nearest water (m)	10.22	(8.9)	9.41	(8.8)	-0.01	(-0.06, 0.04)	0.67
% 30 cm<x<1 m	22.29	(20.5)	22.72	(19.9)	0.003	(-0.02, 0.02)	0.75
% Sedges, grasses, and forbs	39.77	(14.7)	38.42	(14.7)	-0.02	(-0.05, 0.01)	0.26
% Nest cover	15.88	(15.9)	13.12	(12.2)	-0.01	(-0.04, 0.03)	0.71
Male size-adjusted mass	0.96	(4.4)	0.48	(4.2)	-0.11	(-0.31, 0.10)	0.31
Female size-adjusted mass	1.23	(2.1)	0.49	(2.9)	-0.32	(-0.61, -0.02)	**0.03**

Table III. Mean and standard error (SE) of Hudsonian Godwit (*Limosa haemastica*) defensive behaviors within and outside of the Mew Gull (*Larus canus*) colonies in Beluga River, Alaska. β coefficients, 95% confidence intervals (CI), and p-values are derived from GLMM tests.

	Within (n=20)		Outside (n=12)		β	(95% CI)	p-value
	Mean	SE	Mean	SE			
Male present	0.47	(0.13)	0.64	(0.08)	2.44	(0.01, 4.87)	**0.04**
Female present	0.93	(0.12)	0.90	(0.16)	0.26	(-0.78, 1.31)	0.62
Minimum distance the male would approach the observer	6.95	(6.8)	11.53	(11.7)	0.23	(-0.91, 1.38)	0.68
Minimum distance the female would approach the observer	6.14	(7.6)	3.63	(5.3)	-0.76	(-2.37, 0.84)	0.35
Number of calls per minute by the male	40.34	(20.0)	54.7	(8.1)	3.25	(0.07, 6.43)	**0.04**
Number of calls per minute by the female	41.83	(12.7)	38.49	(9.1)	0.39	(-0.89, 1.68)	0.55
Number of flights per minute by the male	2.77	(2.1)	2.70	(1.6)	-0.09	(-1.22, 1.04)	0.88
Number of flights per minute by the female	2.02	(1.7)	2.69	(2.8)	0.75	(-0.76, 2.27)	0.33

Table IV. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and body condition. Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for all Hudsonian Godwit nests found in 2009 – 2012 and 2014 – 2016 within Mew Gull (*Larus canus*) colonies in Beluga River, Alaska. All models include both plot and a linear time trend as additional covariates.

Model	$dAIC_C$	k	Weight
Female condition + % cover between 30 cm and 1 m tall	0.00	5	0.18
Female condition + % sedge, grass, and forb cover	0.46	5	0.14
Female condition + nest cover	0.84	5	0.12
Female condition	1.81	4	0.07
Female condition + male condition + % cover between 30 cm and 1 m tall	2.01	6	0.06
Female condition + male condition + % sedge, grass, and forb cover	2.48	6	0.05
Female condition + male condition + nest cover	2.83	6	0.04
Female condition + distance to closest water	2.93	5	0.04
% cover between 30 cm and 1 m tall	3.57	4	0.03
Female condition + male condition	3.76	5	0.03
% sedge, grass, and forb cover	3.95	4	0.02
Nest cover	4.71	4	0.02
Male condition + % cover between 30 cm and 1 m tall	4.77	5	0.02
Female condition + male condition + distance to closest water	4.79	6	0.02
Null	5.13	3	0.01
Male condition + % sedge, grass, and forb cover	5.32	5	0.01
Distance to closest water	5.64	4	0.01
Male condition + nest cover	6.21	5	0.01
Male condition	6.83	4	0.01
Male condition + distance to closest water	7.48	5	0.00

Table V. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) nest survival, habitat variables, and body condition. Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for all Hudsonian Godwit nests found in 2009 – 2012 and 2014 – 2016 outside of Mew Gull (*Larus canus*) colonies in Beluga River, Alaska. All models include both plot and a linear time trend as additional covariates.

Model	$dAIC_C$	k	Weight
Male condition + nest cover	0.00	5	0.20
Male condition	1.76	4	0.08
Female condition + male condition + nest cover	1.77	6	0.08
Male condition + % sedge, grass, and forb cover	2.49	5	0.06
Male condition + distance to closest water	2.81	5	0.05
Female condition + male condition	3.43	5	0.04
Male condition + % cover between 30 cm and 1 m tall	3.59	5	0.03
Nest cover	3.89	4	0.03
Female condition + male condition + % sedge, grass, and forb cover	3.92	6	0.03
% sedge, grass, and forb cover	4.41	4	0.02
Female condition + male condition + distance to closest water	4.57	6	0.02
Null	4.66	3	0.02
Female condition + male condition + % cover between 30 cm and 1 m tall	5.10	6	0.02
Female condition + nest cover	5.55	5	0.01
% cover between 30 cm and 1 m tall	6.09	4	0.01
Distance to closest water	6.23	4	0.01
Female condition + % sedge, grass, and forb cover	6.39	5	0.01
Female condition	6.62	4	0.01
Female condition + % cover between 30 cm and 1 m tall	8.14	5	0.00
Female condition + distance to closest water	8.21	5	0.00

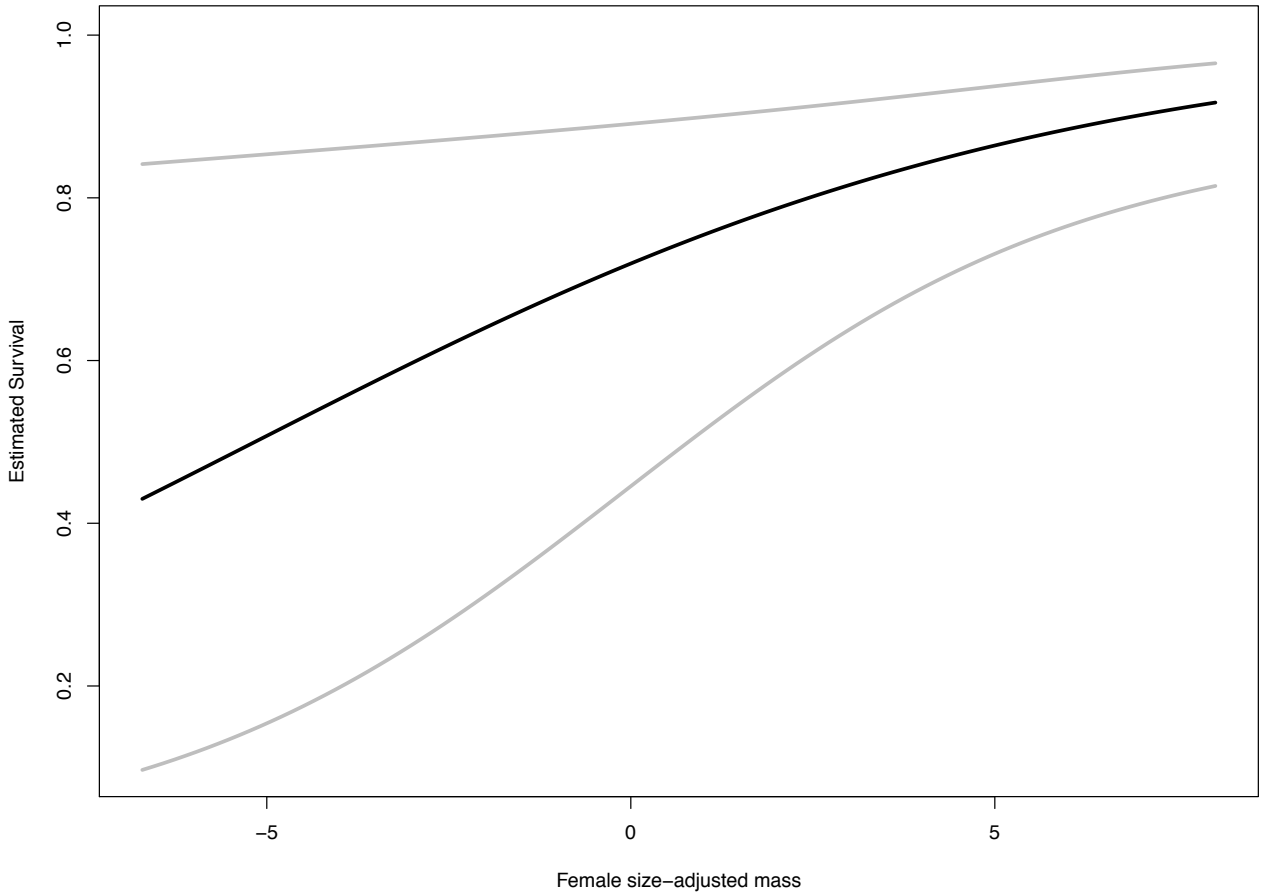

Figure 1. Daily survival rates of Hudsonian Godwit (*Limosa haemastica*) nests within Mew Gull (*Larus canus*) colonies increased with increasing female body condition in Beluga River, Alaska from 2009 – 2016. Ninety-five percent confidence intervals shown (gray lines).

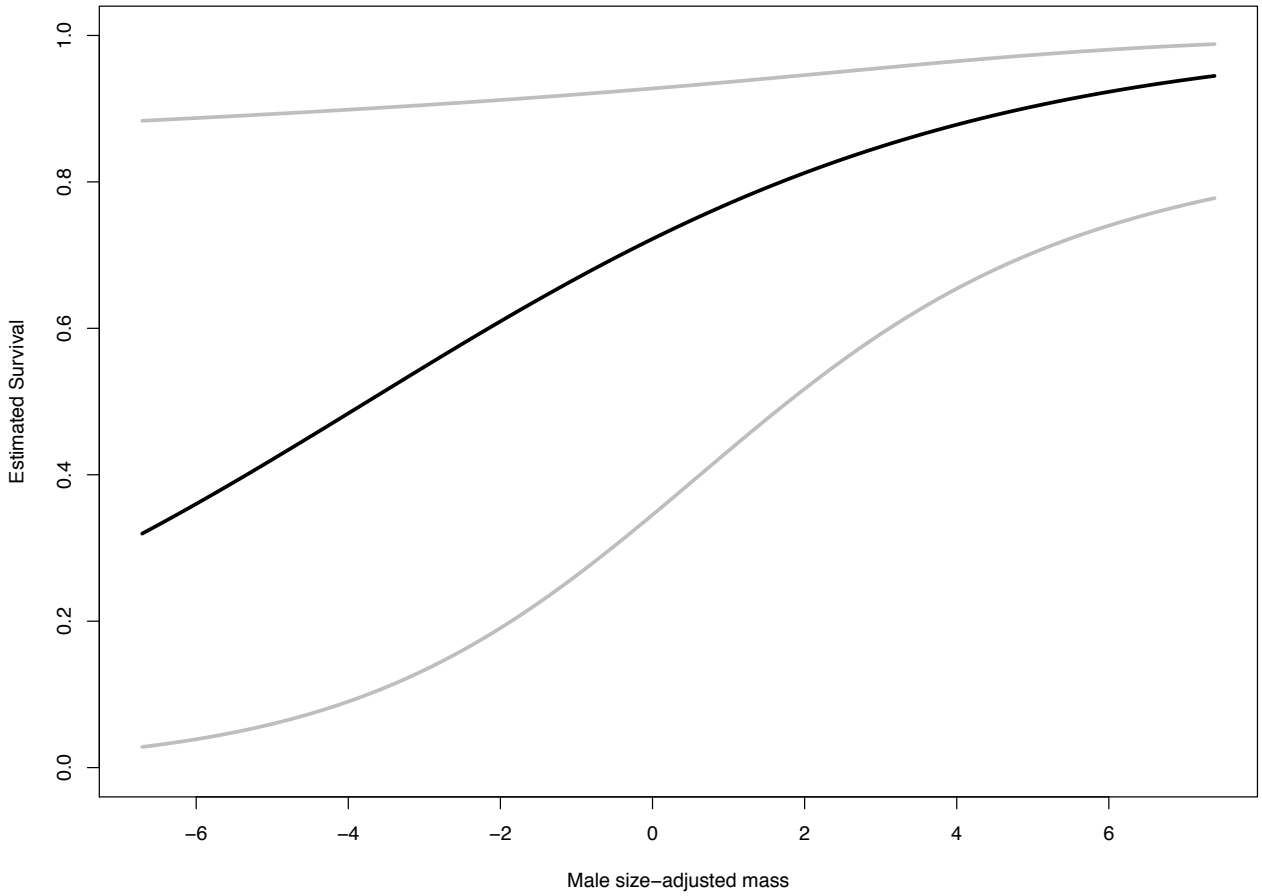

Figure 2. Daily survival rates of Hudsonian Godwit (*Limosa haemastica*) nests outside of Mew Gull (*Larus canus*) colonies increased with increasing male body condition in Beluga River, Alaska from 2009 – 2016. Ninety-five percent confidence intervals shown (gray lines).

APPENDIX C

Table CI. Nest survival, nest site microhabitat characteristics, proximity to Mew Gulls (*Larus canus*), and body condition data for all Hudsonian Godwit (*Limosa haemastica*) nests found in Beluga River, Alaska from 2009 – 2016.

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to water (m)	% 30cm to 1m	% Herb cover	% Overhead nest cover	Male body condition	Female body condition
2009GN001	10	31	31	Hatch	2009	North	0	5.21	21	38	5	4.83	7.39
2009GN002	6	30	30	Hatch	2009	North	0	3.02	30	22	6	-0.30	6.75
2009GN007	15	33	33	Hatch	2009	North	0	12.80	39	47	5	1.62	4.19
2009GN008	27	28	28	Hatch	2009	North	0	6.68	26	47	15	NA	NA
2009GN010	6	28	28	Hatch	2009	North	0	10.88	73	47	5	-2.22	4.83
2009GN012	10	31	31	Hatch	2009	North	0	0.50	60	48	30	6.75	4.83
2009GN013	19	44	44	Hatch	2009	North	983.82	6.43	38	41	10	4.83	7.39
2009GN014	10	29	29	Hatch	2009	North	0	17.31	50	46	30	0.98	2.26
2009GN015	10	10	12	Fail	2009	South	0	NA	NA	NA	NA	NA	NA
2009GN017	8	17	19	Fail	2009	South	62.31	0.36	33	26	20	1.62	6.75
2009GN018	10	12	15	Fail	2009	North	0	16.50	36	46	25	NA	NA
2009GN022	11	33	33	Hatch	2009	North	84.24	9.14	57	50	20	3.55	7.39
2009GN027	15	33	33	Hatch	2009	North	0	8.08	43	31	30	3.55	4.19
2009GN0281	5	17	19	Fail	2009	South	0	5.59	22	36	20	4.83	6.11
2009GN036	18	38	38	Hatch	2009	North	14.52	NA	NA	NA	NA	NA	4.83
2009GN043	10	17	19	Fail	2009	South	0.89	8.02	55	50	10	3.55	6.75
2009GN044	14	28	28	Hatch	2009	North	0	12.92	40	54	25	-5.43	1.62
2009GN045	19	32	32	Hatch	2009	North	450.32	13.72	52	40	35	NA	0.34
2009GN046	19	33	33	Hatch	2009	North	0	0.30	33	45	10	1.62	0.34
2009GN047	21	27	27	Hatch	2009	North	0	3.69	40	38	32	-4.79	NA
2009GN048	27	29	29	Hatch	2009	North	0	0.50	18	45	30	-6.71	-5.43
2009GN049	28	33	33	Hatch	2009	North	0	16.31	43	47	2	-3.50	-2.86
2009GN0282	26	45	45	Hatch	2009	North	0	NA	NA	NA	NA	NA	NA
2010GN07	9	9	10	Fail	2010	North	98.14	3.53	0	20	8	NA	NA
2010GN11	18	41	41	Hatch	2010	North	0	2.67	4	19	15	NA	7.39
2010GN41	7	7	8	Fail	2010	North	0	0.50	12	24	5	NA	NA
2010GN43	9	9	10	Fail	2010	North	0	30.28	15	18	45	NA	NA

TABLE CI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to water (m)	% 30cm to 1m	% Herb cover	% Overhead nest cover	Male body condition	Female body condition
2010GN47	10	34	34	Hatch	2010	South	106.36	3.51	2	26	13	4.19	-0.94
2010GN49	11	11	13	Fail	2010	North	0	18.21	1	20	10	NA	NA
2010GN53	16	33	33	Hatch	2010	South	0	5.03	5	28	5	3.55	3.55
2010GN55	20	20	21	Fail	2010	North	0	1.86	3	21	30	NA	NA
2010GN56	22	22	23	Fail	2010	North	194.49	4.52	8	20	8	NA	NA
2010GN57	17	17	19	Fail	2010	North	176.65	4.70	12	20	10	NA	NA
2010GN58	23	43	43	Hatch	2010	North	0	18.59	5	21	25	-0.94	6.11
2010GN61	30	31	31	Hatch	2010	South	82.99	0.50	4	20	25	-6.71	NA
2010GNHUYU	1	29	29	Hatch	2010	South	87.92	1.93	10	21	35	6.75	-2.22
2010GNHX2	13	38	38	Hatch	2010	North	0	1.65	4	28	5	7.39	6.11
2010GNHXXC	4	6	9	Fail	2010	North	0	11.07	13	18	5	NA	NA
2010GNKX	13	30	30	Hatch	2010	North	0	16	15	22	25	2.26	4.19
2010GNPE	7	7	9	Fail	2010	North	0	10.49	1	24	25	NA	NA
2010GNPEJA	14	41	41	Hatch	2010	North	0	NA	8	15	10	1.62	6.75
2010GNPK	20	46	46	Hatch	2010	North	0	12.98	1	26	35	6.75	8.03
2010GNPM	43	44	44	Hatch	2010	North	0	5.06	5	27	17	NA	NA
2010GNUL	2	30	30	Hatch	2010	North	0	13.51	3	20	5	7.39	5.47
2010GNXKTV	14	26	27	Fail	2010	North	450.32	10.14	5	20	43	0.98	2.26
2010GNYMXV	29	30	30	Hatch	2010	North	0	17.12	22	15	43	-6.71	-6.71
2010GNYN	6	6	7	Fail	2010	North	38.2	11.17	2	17	5	NA	NA
2010GNYN2	22	46	46	Hatch	2010	North	0	1.60	2	46	5	7.39	NA
2010GNYTXL	7	27	27	Hatch	2010	South	0	4.19	18	44	15	4.83	NA
2010GNYV	6	6	7	Fail	2010	North	0	20.32	10	32	20	NA	NA
2010GNYV2	14	20	24	Fail	2010	North	0	2.36	8	30	5	5.47	7.39
2011GN08	21	44	44	Hatch	2011	North	0	8.50	15	54	6	5.47	7.39
2011GN10	27	33	33	Hatch	2011	North	0	12.56	1	39	25	-3.50	-3.50

TABLE CI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to water (m)	% 30cm to 1m	% Herb cover	% Overhead nest cover	Male body condition	Female body condition
2011GN12	28	42	44	Fail	2011	North	10.11	7.80	2	42	2	5.47	2.26
2011GN13	35	38	38	Hatch	2011	North	0	6.13	25	47	5	NA	NA
2011GNAPAU	34	35	35	Hatch	2011	North	0	7.47	30	24	40	-6.71	NA
2011GNC4MJ	6	33	33	Hatch	2011	North	92.8	8.53	20	48	1	4.83	NA
2011GNCC	7	14	16	Fail	2011	North	0	16.57	5	73	25	NA	NA
2011GNCT	32	33	33	Hatch	2011	North	0	0.21	20	13	4	NA	NA
2011GNE5E9	26	41	41	Hatch	2011	North	0	1.16	5	64	1	2.26	2.26
2011GNEAE7	6	32	32	Hatch	2011	North	0	9.75	35	48	10	4.83	6.11
2011GNH7T2	19	40	40	Hatch	2011	North	0	7.62	70	45	10	6.75	6.11
2011GNH8L0	8	29	29	Hatch	2011	South	0	8.60	20	57	10	2.91	4.19
2011GNJMXH	13	17	19	Fail	2011	South	31.13	4.66	65	55	15	NA	NA
2011GNJTMU	37	38	38	Hatch	2011	North	444.42	9.63	30	59	30	-6.71	-6.07
2011GNK0PM	20	31	31	Hatch	2011	North	0	13.17	60	55	4	0.34	0.34
2011GNK4T7	15	31	31	Hatch	2011	South	232.07	25.82	40	48	25	1.62	2.91
2011GNK5L4	27	34	35	Fail	2011	North	69.03	11.58	30	39	0	-0.94	-1.58
2011GNL5E6	20	31	33	Fail	2011	South	23.67	24.94	65	49	5	4.19	4.19
2011GNM2P2	14	31	31	Hatch	2011	North	0	8.02	20	61	10	3.55	4.83
2011GNM3U0	19	35	35	Hatch	2011	North	0	16.67	4	45	5	3.55	3.55
2011GNN8X3	7	34	34	Hatch	2011	North	0	8.08	20	64	15	6.75	5.47
2011GNTANA	30	31	31	Hatch	2011	North	0	7.74	70	38	17	NA	NA
2011GNV9C0	22	37	37	Hatch	2011	North	0	16.28	10	31	18	0.34	2.26
2011GNX5OH	8	30	30	Hatch	2011	North	0	6.71	75	43	40	4.19	5.47
2011GNX6H3	6	29	29	Hatch	2011	North	0	5.43	10	56	25	4.19	7.39
2011GNXA	12	12	14	Fail	2011	North	127.49	3.66	60	64	10	NA	NA
2011GNY0T4	13	22	24	Fail	2011	South	0	29.26	55	59	10	4.83	4.83
2011GNY9L6	14	34	34	Hatch	2011	North	0	12.01	20	37	7	1.62	4.19

TABLE CI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to water (m)	% 30cm to 1m	% Herb cover	% Overhead nest cover	Male body condition	Female body condition
2012GN1MNNV	11	31	31	Hatch	2012	South	137	NA	NA	NA	NA	6.75	NA
2012GNC8J2	4	8	9	Fail	2012	North	0	NA	NA	NA	NA	8.03	NA
2012GNCT	10	33	33	Hatch	2012	North	0	NA	NA	NA	NA	7.39	7.39
2012GNEE	12	33	33	Hatch	2012	North	0	NA	NA	NA	NA	6.11	6.75
2012GNH7T2	6	10	11	Fail	2012	North	0	NA	NA	NA	NA	NA	NA
2012GNH8L0	7	12	15	Fail	2012	South	0	NA	NA	NA	NA	NA	6.75
2012GNJMMH	10	14	17	Fail	2012	South	30.65	NA	NA	NA	NA	NA	NA
2012GNK4MH	7	33	33	Hatch	2012	South	320.33	NA	NA	NA	NA	7.39	NA
2012GNL5	17	17	19	Fail	2012	South	0	NA	NA	NA	NA	NA	NA
2012GNM2P2	6	7	8	Fail	2012	North	0	NA	NA	NA	NA	NA	NA
2012GNM2P2R	20	20	21	Fail	2012	North	107.09	NA	NA	NA	NA	NA	NA
2012GNM3U0	8	8	10	Fail	2012	North	0	NA	NA	NA	NA	NA	NA
2012GNN62	27	29	31	Fail	2012	North	439.37	NA	NA	NA	NA	NA	NA
2012GNN8X3	8	33	33	Hatch	2012	North	0	NA	NA	NA	NA	8.67	7.39
2012GNTANA	6	30	30	Hatch	2012	North	0	NA	NA	NA	NA	NA	5.47
2012GNX50H	7	33	33	Hatch	2012	North	0	NA	NA	NA	NA	8.03	7.39
2012GNX6H3	10	10	11	Fail	2012	North	0	NA	NA	NA	NA	NA	NA
2012GNX8	26	33	33	Hatch	2012	North	0	NA	NA	NA	NA	-0.94	-2.22
2012GNY9	21	26	28	Fail	2012	North	0	NA	NA	NA	NA	NA	NA
2014HUGOBHD11	20	32	32	Hatch	2014	South	0	1.30	0	50	10	NA	NA
2014HUGOBHD17	33	47	47	Hatch	2014	South	0	0.25	0	66	1	0.34	NA
2014HUGOBHD19	38	43	43	Hatch	2014	North	0	14.40	3	29	8	NA	-4.14
2014HUGOBJL17	14	31	31	Hatch	2014	North	155.91	3.50	8	38	25	NA	NA
2014HUGOBJL18	18	39	39	Hatch	2014	North	0	0.50	3	34	10	-3.50	NA
2014HUGOBJL19	22	34	34	Hatch	2014	North	0	7.50	3	44	5	NA	-2.86
2014HUGOBJL23	30	31	31	Hatch	2014	North	1	11.25	5	23	10	NA	NA

TABLE CI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to water (m)	% 30cm to 1m	% Herb cover	% Overhead nest cover	Male body condition	Female body condition
2014HUGOBJL25	31	32	32	Hatch	2014	South	0	5.25	3	68	1	NA	NA
2014HUGOGJM06	16	35	35	Hatch	2014	South	61.82	0.25	15	52	5	NA	NA
2014HUGOGJM17	37	38	38	Hatch	2014	North	0	7.75	0	42	5	NA	NA
2014HUGORJS27	35	35	37	Fail	2014	North	0	9.25	2	64	80	NA	NA
2015HUGOGJM05	3	26	26	Hatch	2015	North	0	8.25	30	60	25	-2.86	4.19
2015HUGOGJM18	7	27	27	Hatch	2015	South	95.72	0.50	30	40	5	1.62	4.19
2015HUGOGJM35	11	26	26	Hatch	2015	North	0	25.50	15	44	2	-4.14	-0.30
2015HUGOGJM36	12	35	35	Hatch	2015	South	0	0.65	0	55	10	8.03	5.47
2015HUGOGJM56	18	25	25	Hatch	2015	North	0	13.60	30	45	15	-2.86	-3.50
2015HUGOJAK05	4	29	29	Hatch	2015	North	0	9.98	45	29	5	6.11	1.62
2015HUGOJAK21	8	29	29	Hatch	2015	North	0	1.45	40	32	10	1.62	-1.58
2015HUGOJMH10	7	32	32	Hatch	2015	South	35.74	28.30	20	39	1	-0.30	2.91
2015HUGOJMH15	10	10	10	Fail	2015	North	352.56	7.75	5	54	10	NA	NA
2015HUGOJMH20	11	29	29	Hatch	2015	North	0	16.30	40	37	15	-2.22	2.26
2015HUGOJMH28	15	27	27	Hatch	2015	North	47.46	7.25	40	40	35	-0.94	-0.94
2015HUGOJMH120	40	40	40	Hatch	2015	South	83.54	12.50	10	40	15	NA	NA
2015HUGOKJP11	6	26	26	Hatch	2015	North	0	13.50	60	69	30	-2.86	4.83
2015HUGOKJP18	7	26	26	Hatch	2015	South	0	8.00	15	64	3	0.98	3.55
2015HUGOKJP44	15	27	27	Hatch	2015	North	0	55.30	30	25	15	-4.14	0.98
2015HUGORJS05	22	35	35	Hatch	2015	North	0	8.40	20	45	10	-3.50	0.98
2016HUGOKRS48	18	24	24	Hatch	2016	North	0	18.25	60	35	2	-4.79	-2.86
2016HUGOKRS63	24	24	25	Fail	2016	North	397.62	0.99	10	35	3	NA	NA
2016HUGOLKF04	3	26	26	Hatch	2016	South	4.28	4.25	12	50	2	-4.79	4.83
2016HUGOLKF15	9	26	27	Fail	2016	North	0	21.30	50	20	7	1.62	0.34
2016HUGOLKF22	14	32	32	Hatch	2016	South	181.24	27.50	0	75	1	-0.30	2.26
2016HUGOLKF23	15	22	24	Fail	2016	North	4.88	7.65	20	40	5	1.62	NA

TABLE CI (CONTINUED)

Nest	Day found	Last day active	Last day visited	Nest fate	Year	Plot	Distance to gull colony (m)	Distance to water (m)	% 30cm to 1m	% Herb cover	% Overhead nest cover	Male body condition	Female body condition
2016HUGOMLS14	6	24	24	Hatch	2016	North	0	16.25	25	29	10	-1.58	2.91
2016HUGOMLS37	14	32	32	Hatch	2016	South	295.37	4.30	8	45	0	-2.86	2.91
2016HUGORIG01	4	4	6	Fail	2016	North	105.4	5.50	8	36	1	NA	NA
2016HUGORIG15	16	37	37	Hatch	2016	North	0	3.45	5	40	3	4.83	-4.79
2016HUGORJS01	1	4	7	Fail	2016	North	152.07	4.85	30	46	5	NA	NA
2016HUGORJS02	4	10	13	Fail	2016	North	0	5.30	8	35	60	NA	2.91
2016HUGORJS04	7	27	27	Hatch	2016	North	0	38.5	35	20	85	6.11	4.19
2016HUGORJS07	10	27	27	Hatch	2016	North	0	4.00	2	41	3	-0.94	1.62
2016HUGORJS10	12	27	27	Hatch	2016	South	211.02	20.50	18	23	3	-2.22	2.26
2016HUGORJS16	26	29	29	Hatch	2016	South	210.32	28.60	15	22	6	-4.14	-4.79

Table CII. Defensive behaviors data for all Hudsonian Godwit (*Limosa haemastica*) nests found in Beluga River, Alaska in 2015 and 2016.

	Male present	Female present	Male approach distance	Female approach distance	Male calls	Female calls	Male flights	Female flights
2015HUGOGJM05	0.50	1.00	20.00	4.50	0.00	55.50	0.00	2.50
2015HUGOGJM18	0.50	1.00	5.00	14.75	48.00	42.50	4.00	1.50
2015HUGOGJM35	0.50	1.00	2.00	2.00	30.00	43.50	2.00	1.50
2015HUGOGJM36	1.00	0.00	11.00	NA	70.50	NA	1.00	NA
2015HUGOGJM56	NA	NA	NA	NA	NA	NA	NA	NA
2015HUGOJAK05	1.00	1.00	6.92	21.67	36.00	14.50	3.33	1.00
2015HUGOJAK21	1.00	1.00	3.50	4.42	38.33	32.00	2.50	1.83
2015HUGOJMH10	0.00	1.00	NA	5.00	NA	29.00	NA	1.50
2015HUGOJMH15	NA	NA	NA	NA	NA	NA	NA	NA
2015HUGOJMH20	0.66	1.00	23.75	1.83	5.00	15.17	0.50	2.17
2015HUGOJMH28	1.00	1.00	0.50	0.50	60.00	55.00	5.00	3.50
2015HUGOJMH120	NA	NA	NA	NA	NA	NA	NA	NA
2015HUGOKJP11	0.50	1.00	2.50	1.00	38.00	42.25	2.00	0.75
2015HUGOKJP18	0.33	1.00	3.00	1.03	53.50	45.33	3.50	1.33
2015HUGOKJP44	1.00	1.00	10.50	0.63	31.50	54.00	2.75	0.75
2015HUGORJS05	0.66	1.00	2.00	7.67	23.50	61.17	2.25	1.67
2016HUGOKRS48	0.75	1.00	6.50	22.50	47.37	40.10	2.33	0.50
2016HUGOKRS63	NA	NA	NA	NA	NA	NA	NA	NA
2016HUGOLKF04	0.50	0.50	0.50	0.02	61.00	46.50	6.80	7.10
2016HUGOLKF15	0.00	1.00	NA	20.00	NA	41.00	NA	0.40
2016HUGOLKF22	1.00	0.75	9.67	0.13	67.20	41.23	2.87	8.23
2016HUGOLKF23	1.00	1.00	10.00	1.00	66.00	49.40	0.20	1.40
2016HUGOMLS14	0.00	1.00	NA	5.33	NA	46.07	NA	2.80
2016HUGOMLS37	0.60	0.80	32.00	0.50	44.80	33.80	0.70	3.60
2016HUGORIG01	NA	NA	NA	NA	NA	NA	NA	NA
2016HUGORIG15	0.66	1.00	2.00	3.25	40.50	39.35	4.20	1.55
2016HUGORJS01	NA	NA	NA	NA	NA	NA	NA	NA
2016HUGORJS02	NA	NA	NA	NA	NA	NA	NA	NA
2016HUGORJS04	0.66	1.00	7.00	5.58	61.00	52.15	3.40	2.30
2016HUGORJS07	0.75	1.00	0.08	2.00	43.36	33.13	7.48	4.87
2016HUGORJS10	1.00	1.00	18.00	4.50	53.80	38.90	1.50	0.50
2016HUGORJS16	1.00	1.00	4.00	0.00	54.40	29.00	2.00	0.00

CHAPTER FOUR

RISKS AND REWARDS OF FORAGING PATCHES FOR A NON-BREEDING SHOREBIRD

Abstract:

Patchily-distributed resources require individuals to balance the risks and rewards of selecting and moving among alternative patches. Risks and rewards can vary among patches because the overall quality of a foraging patch reflects not only its food availability, but also levels of exposure to human disturbances and predators that can reduce the time an individual can actively forage. We conducted 147 surveys of 42 intertidal mudflats in the region of Chiloé Island, Chile to assess the relative influence of foraging success, availability of intertidal foraging habitat, landscape and bay characteristics, human disturbances, and predation risk on flock density and body condition of Hudsonian Godwits (*Limosa haemastica*) during the non-breeding season. Our results suggest that patch quality was determined not only by the foraging habitat (i.e., substrate availability, success rates), but also, by perceived risks. Specifically, increasing availability of foraging habitat and foraging success increased flock densities and body condition in godwits, but bays where individuals were more alert and agitated had smaller flock densities in poorer condition. Our findings suggest important non-lethal effects of disturbances, such that increased scanning rates and displacement flights have the potential to compromise refueling rates and body condition and can affect performance across seasons. Thus, the quality of foraging patches during the non-breeding season may have far-reaching consequences for individuals and populations, potentially affecting their survival and future reproductive success.

Keywords: human disturbance, non-lethal effects, foraging success, predation risk, shorebirds

Introduction:

Most animals must select among foraging patches that differ in potential energy gain, competition, risk of predation and disease, and exposure to weather, disturbance, or other threats (Fretwell and Lucas 1970, Lima and Dill 1990, Piersma 2012). Migratory species, such as shorebirds, are especially challenged to identify the most profitable patches in sometimes unfamiliar habitats that they encounter during their trans-hemispheric migrations. Previous research on migratory shorebirds during the non-breeding season has demonstrated that land conversion, human disturbances, competition for food resources, and predation risk can all impact habitat quality and use (Burger and Gochfeld 1991, Nebel and Ydenberg 2005, Fernández and Lank 2008). However, the role of each of these factors is typically studied independently making it difficult to measure overall habitat quality. Instead, the density of individuals is often considered a proxy for habitat quality (Fretwell and Lucas 1970) then used to understand the relative influence of foraging success and predation risk on foraging individuals. Our ability to understand foraging decisions of shorebirds is therefore, in part, constrained by our ability to measure habitat quality.

Among the many factors that may influence the foraging decisions of shorebirds, food availability is one of the most essential (Kelsey and Hassall 1989, Finn et al. 2008). Individuals generally show high fidelity to patches with consistent levels of food availability (Folmer et al. 2010, Rutten et al. 2010), and many species aggregate in response to the distribution of their preferred prey at non-breeding and stopover sites (Goss-Custard 1970, Colwell and Landrum 1993, Rose and Nol 2010). Additionally, foraging substrate can influence the availability of prey and, thus, habitat use (Finn et al. 2008). For example, the foraging site choices of Far Eastern Curlews (*Numenius madagascariensis*) are strongly affected by substrate resistance, and both

curlews and their prey are most abundant on substrates with little or no hard material (rocks, coral, shell grit; Finn et al. 2008). Foraging success is particularly important for migratory shorebirds during the non-breeding season, as one of their primary concerns during this period is fueling in recovery from, or preparation for, long-distance migration (Piersma 1997, Battley et al. 2003, 2004, Kvist and Lindstrom 2003). Individuals foraging in patches with high densities of food or higher intake rates can accumulate mass more quickly, thereby minimizing foraging time and improving their overall body condition (Duijns et al. 2009). As such, the distribution and density of available prey can influence both foraging site choice and, ultimately, the condition of shorebirds.

Perceived or actual threats from human activity or predators also influence the abundance, behavior, distribution, and condition of individuals. Shorebirds often minimize time spent foraging in close proximity to habitats that may conceal predators (Pomeroy 2006, Yasué 2006), and may completely avoid foraging in areas with high risk of predation (Hilton et al. 1999). Foraging shorebirds also employ a suite of behaviors to further minimize predation risk, including assembling in large groups and maintaining vigilance (Elgar 1989, Cresswell 1994a, Bednekoff and Lima 1998). Because shorebirds can also perceive humans as predators (Frid and Dill 2002), human disturbances can influence shorebird habitat use and behavior through reductions in time devoted to foraging, increased time spent scanning, and displacement from foraging areas (Pfister et al. 1992, Yasué 2005, Burger et al. 2007, Schlacher et al. 2014). Shorebirds may respond even more strongly to the presence of dogs, often avoiding areas frequented by dogs (Thomas et al. 2003, Burger et al. 2007). In turn, anti-predator behaviors, such as increased time spent scanning for predators, may negatively impact body condition, especially when food is limited (Goss-Custard et al. 2006). Disturbances can result in lost

foraging time and extra energy expenditure and, therefore, affect individual performance (Yasué 2005, Goss-Custard et al. 2006).

Because body condition can influence an individual's performance, the quality of a patch occupied by an individual during the nonbreeding season can ultimately affect its survival and reproductive success (Fernández and Lank 2006, Norris and Marra 2007, Cooper et al. 2015). Understanding the impacts of non-breeding patch quality on individual condition may therefore help inform conservation efforts (Sheehy et al. 2010). In our study, we evaluated how patch attributes affected habitat quality for a long-distance migratory shorebird, the Hudsonian Godwit (*Limosa haemastica;* hereafter: godwits), during the non-breeding season on Chiloé Island and the adjacent mainland in southern Chile. Hudsonian Godwits are among the most rapidly declining shorebird species in North America, with an annual rate of decline of 3.45% over the last 30 years (Smith et al. unpubl. data). As a result, understanding how habitat quality during the non-breeding season may limit or otherwise affect godwit populations is a high priority (Senner 2010).

Unlike most previous research that has examined individual drivers of habitat quality, we simultaneously estimated the direct and indirect influence of human disturbances, predation risk, landscape and bay characteristics, foraging success, and amount of foraging habitat on flock density and body condition of godwits. Specifically, we asked what is the relative influence of foraging success, amount of foraging habitat, landscape and bay characteristics, predation risk, and human disturbance on habitat quality, flock density, and body condition of godwits? We predicted that (1) godwits would be in the best condition and at the highest densities at intertidal mudflats with less human disturbance, low predation risk, high foraging success, and abundant

foraging habitat, and that (2) godwits would be more sensitive to human disturbances and predation risk than foraging success and habitat availability.

Methods:

Study Species:

Chiloé Island and the adjacent mainland (~42°30'S, 73°45'W), in the Los Lagos province of Chile, support the largest non-breeding population of Hudsonian Godwits on the Pacific coast of South America (Senner and Angulo-Pratalongo 2014, García-Walther et al. 2017). Godwits aggregate in large flocks in shallow bays with extensive intertidal mudflats from October to April during their non-breeding season (Espinosa et al. 2005, Andres et al. 2009). Connectivity and movements of individual godwits within the Chiloé region are poorly understood, but individuals are known to move among bays in the central part of the island due to disturbances, predators, the tide, and weather (Andres et al. 2009). Additionally, color-marked individuals have been resighted moving among bays separated by as much as 40 km (NR Senner and RJ Swift unpubl. data).

Godwits spend over half of the year on the non-breeding grounds (Senner et al. 2014). Following the non-breeding season, during northbound migration, godwits undertake an extreme non-stop flight to the Great Plains of the United States, flying over 10,000 km in roughly seven days en route to their breeding grounds in Alaska (Senner et al. 2014). Upon arrival to the breeding grounds, most individuals initiate egg laying within seven days – a rapid transition from the non-breeding season. As such, individuals may utilize reserves from the non-breeding grounds or stopover sites in order to initiate breeding (Guillemain et al. 2008).

Study Area:

Foraging godwits use intertidal mudflats along the mainland Chilean coast near Puerto Montt, on Chiloé Island, and on a number of smaller islands in the Gulf of Corcovado; most sites with large concentrations of godwits occur on Chiloé Island itself (Figure 1; Morrison and Ross 1989, García-Walther et al. 2017). However, the distribution of godwits across the island is not uniform. The island's western and southern coasts are relatively inaccessible and are thought to be largely unused by godwits because of their steep, rocky coastlines and extensive sandy beaches. In contrast, the northern and eastern coastlines, which consist of many bays with intertidal mudflats, support most of the island's human population, agriculture, and aquaculture (Morrison and Ross 1989, García-Walther et al. 2017).

Potential Disturbances:

The number of potential anthropogenic disturbances in the Chiloé region are myriad, as Chilean law protects neither the intertidal habitats nor godwits themselves, and all shorelines are publicly accessible, with small towns or cities frequently situated nearby (Andres et al. 2009, Delgado et al. 2010). Many Chiloé residents thus utilize the intertidal mudflats, especially for subsistence and commercial harvests of algae and shellfish. Previous work showed human activities impact how godwits use bays (Andres et al. 2009). For example, counts of godwits at a bay on the northern coast of the island, Caulín, were low (<300 individuals) in January 2006 when 225 people were observed harvesting farmed algae on the mudflats, while counts of godwits in previous years were typically much larger (>1,000 individuals; Andres et al. 2009).

The primary natural predator of godwits in the region is the Peregrine Falcon (*Falco peregrinus*), although foraging godwits occasionally also flush in response to Southern Caracaras

(*Caracara plancus*; RJ Swift unpubl. data). Peregrine Falcons are relatively uncommon, however, and occurred at only 5 of 42 bays we visited (RJ Swift unpubl. data). Additionally, only single individual falcons were ever seen at one time.

Field Surveys and Flock Counts:

We attempted to survey all known and accessible bays in the Chiloé Island region based on published accounts, eBird records, and prior knowledge of the distribution of godwits. In total, we surveyed 42 bays between 1 January and 9 March 2016 (Figure 1). We conducted surveys (n = 147) within three hours of the diurnal low tide on days with light winds (<20 km/hour) and little or no precipitation. The length of each scan varied (range 5 – 365 minutes, μ = 85 ± 86.9; all means presented ± SD), based on the presence and size of the godwit flock, the amount of available daylight, and the height of the tide. Each site was visited between one and nine times (μ = 3.5 ± 1.8; Table I), with two bays (Huildad and Chamiza-Norte) being visited only once due to poor weather conditions.

The same two observers conducted all surveys using binoculars and spotting scopes equipped with a 20-60x eyepiece. We maximized detection of godwits by making observations from locations that provided complete visibility of each bay but which also prevented direct disturbance of the foraging flock. For each survey period, we recorded flock size and behavioral state (flying, foraging, or roosting). We classified godwits as foraging when they were probing and moving (e.g., with the advancing or receding tide), or as roosting if they remained stationary (typically with one leg up and heads tucked under their wings) and did not probe. Surveys in which most godwits were roosting rather than foraging were excluded from analyses. During the surveys, one observer carefully counted or estimated the godwit flock at least once each hour.

From these counts, we present a maximum density observed, adjusted by each bay's perimeter at the high tide line (generated using Google Earth Pro v. 7.1.5) to account for size differences among bays. If no godwits were present at the start of a survey, we waited from 5 – 60 minutes for godwits to arrive ($\mu = 22 \pm 21$ minutes).

Body Condition:

We collected two measures of body condition: body molt scores (BMS) and abdominal profile indices (API). The BMS is an index between zero and four (with 0.5 increments) based on the amount of alternate plumage present on an individual (e.g., Piersma and Jukema 1993). As body feathers represent up to 75% of total feather mass (Battley and Piersma 1997, 2005) and replacement of these feathers implies a significant metabolic cost associated with feather production and thermoregulation (Klaassen 1995), body molt scores were used as an indicator of individual condition (e.g., Lourenço and Piersma 2015). API is a measure of condition based on the shape of the abdomen and is correlated with actual fat mass in shorebirds (Wiersma and Piersma 1995).

Individual BMS and API were collected between one and four times per survey (depending on the flock size and the length of the survey) on a total of 1 – 76 individuals ($\mu = 24 \pm 14.5$). For large flocks (>20 individuals), BMS and API were taken for every fifth or tenth individual for which visibility and proximity allowed careful scoring. We assessed every individual in smaller flocks. The residuals from separate regressions of average BMS and API with Julian date were used in analyses to account for continuous molting and pre-migratory fattening.

Foraging Success and Intertidal Foraging Habitat:

We conducted focal foraging observations at each bay with actively foraging godwits (n = 429). Using a voice recorder, we dictated our observations of godwit behaviors over a five-minute period and later transcribed recordings using CowLog (Pastell 2016). Because not all focal observations lasted for the full five minutes (e.g., an individual flew out of sight, reshuffled into the foraging flock such that we lost it, or began roosting), we converted all metrics to the number-per-minute-of-observation. We randomly selected individuals that were feeding within two meters of the tideline and followed them, dictating every behavior including: the number of probes made, the number of prey items captured and consumed (swallowed), and the number of alert or vigilant behaviors displayed. We attempted to follow at least five individuals per survey, although this varied due to the tidal conditions, the presence of foraging godwits, and the total number of godwits in a flock (range = 1 – 13 focal observations, $\mu = 5.17 \pm 2.6$ per survey).

We defined a foraging probe as occurring when at least half of an individual's bill was placed in the mud. Godwits frequently probe the mud in rapid succession without removing their bill; in these circumstances, we counted each movement as a separate probe if the bill was lifted one-third of the way out of the mud (Senner and Coddington 2011). We considered a bird to have obtained a prey item when we discerned a swallowing motion or saw an item in its bill. While godwits feed primarily on relatively large and easily observable polychaete worms (Ieno et al. 2000), godwits also feed on small items, such as fly larvae (Ribeiro et al. 2004, Senner and Coddington 2011, Walker et al. 2011). Such smaller food items can be consumed without removing the entirety of an individual's bill from the mud and would not have been counted in our swallow or success rate estimates. Consequently, our estimates of foraging success represent a minimum level.

At the end of each focal observation, we recorded the primary foraging substrates used during the observation. From 289 focal observations where godwits foraged outside of standing water, godwits primarily used mud (n = 127) or algae (n = 149) as their foraging substrates. Combined, mud and algae account for ~96% of the known foraging substrates, and thus the combined amount of mud and algae was considered appropriate foraging habitat for analyses. Godwits occasionally foraged on both shellfish beds (n = 8) and in rocky areas (n = 5), but only at bays where more rock or shellfish were more available than average and, typically, more plentiful than mud or algae.

From 1 February to 8 March, we estimated the approximate percentage of the tideline covered by each of the four intertidal substrates (mud, rock, algae, and shellfish) between one and twelve times depending on the length of survey ($\mu = 3.2 \pm 2.3$; collected every thirty minutes to an hour). The intertidal habitat of each bay was characterized on one to three different days ($\mu = 1.6 \pm 0.7$ days). Because intertidal habitat data were not collected at bays surveyed in January, we averaged the percent mud and algae throughout survey days, as the amount of non-foraging habitat (rock and shellfish) was presumed to be stable across this period.

Human Disturbances and Predation Risk:

During each survey, we recorded the presence of potential predators. We noted the species and number of individual predators as well as their behavior (e.g., flyover or perch) to derive the number of predator species and individuals present. In order to assess the type, amount, and length of human disturbances during each survey, we counted the number of humans, dogs, hoofed animals (typically oxen and horses), and boats that were present within the intertidal area, within 5 m of the tideline, and 100 m of foraging godwits once every hour.

Because the length of each survey varied, we assessed disturbances from 1 – 10 times ($\mu = 2.6 \pm 1.8$; Table II).

During focal foraging observations, we also recorded the number of alert or vigilant behaviors exhibited by an individual, which we defined as non-foraging head movements (e.g., standing still, looking from side to side, or turning the head to scan the sky; see Nol et al. 2014). Finally, we recorded instances in which at least half of all godwits present in a bay flushed. We did not attempt to determine the cause (e.g., human or predator) for each displacement flight.

All counts were divided by the length of the survey (minutes) for use in analyses. To derive a single estimation for each variable, we averaged each variable across individuals or measures for each survey.

Landscape and Bay Characteristics:

For each bay, we collected various land and water use metrics at the landscape scale (Table III). The distance to the nearest road was calculated using Google Earth Pro, and the substrate of the road was recorded in the field. We recorded the presence of and distances to aquaculture activities (both shellfish and salmon) in the bay, and estimated the percent of the visible bay that was covered by aquaculture activities. Lastly, we calculated three measures of bay size in Google Earth Pro: the approximate intertidal area, the length of the bay's perimeter (highest high tideline), and the bay's width (high tideline to water line).

Data Analysis:

Relationships among human disturbance, predation risk, foraging success, amount of intertidal habitat, landscape and bay characteristics, and the flock density and body condition of

godwits were modeled with partial least squares path model (PLS-PM). PLS-PM is a type of path analysis used to explore multiple relationships between blocks of variables and quantify their respective weights (Lleras 2005, Tenenhaus et al. 2005). This statistical method has only recently been applied to ecological datasets (e.g., Puech et al. 2015), but we selected it over covariance-based structural equation modeling approaches because it does not require a large dataset to perform optimally and because it produces values for each latent variable (Chin and Newsted 1999, Chin 2010).

PLS-PM consists of two sub-models called the inner and outer models (Sanchez 2013). The outer model describes relationships between a set of observed variables ('manifest variables') and a synthetic 'latent variable' that is built from these manifest variables. A latent variable cannot be measured directly and is representative of a concept (e.g., habitat quality). For example, the manifest variables 1) 'number of humans present', 2) 'number of humans within 5 m of tideline', and 3) 'number of humans within 100 m of godwits' were used to approximate the latent variable 'human disturbance'. The group formed by a latent variable and its associated manifest variable(s) is called a block. The inner model describes relationships between latent variables, and these relationships are treated as linear regressions. A fitted PLS-PM produces standardized path coefficients for all paths (i.e., direct and indirect effects) that normally range from -1 to 1. These path coefficients are equivalent to standardized regression coefficients, but have the advantage of specifying whether the relationship between latent variables has a positive or negative slope.

Our PLS-PM contained thirteen latent variables (Figures 2, 3). In the preliminary PLS-PM, all potential manifest variables were included when constructing latent variables. However, before obtaining the final model, we made a set of verifications and transformations, as advised

by Sanchez (2013). First, we checked the unidimensionality of each reflective block with Cronbach's alpha and Dillon–Goldstein's rho (Table IV). We changed the sign of variables having negative weights to only integrate positively correlated variables in the same block. Then, we examined the loadings – i.e., the correlations between a latent variable and its manifest variables (Table V). A manifest variable was only retained if 50% of the variability in the manifest variable (i.e., factor loading > 0.7) was captured by the latent variable (Sanchez 2013). We retained some individual variables that met unidimensionality but had loadings < 0.7, which we acknowledged as an acceptable trade-off between model quality and meaningfulness. Cross-loadings allowed us to verify if the shared variance within a block was larger than with other blocks and were assessed similarly. Finally, the overall robustness of models was evaluated with coefficient-of-determination (R^2) and Goodness of Fit (GoF) criterions and a bootstrapping procedure (n = 999). Ninety-five percent confidence intervals that did not encompass zero were considered statistically significant. For PLS-PM, R^2 values for inner models are classified in three categories: low: $R^2 < 0.3$, moderate: $0.3 < R^2 < 0.6$, and high: $R^2 > 0.6$ (Sanchez 2013). The GoF measure assesses the overall predictive performance of both the inner and outer models (Sanchez 2013). Analyses were conducted using the R 3.4.3 software (R Core Development Team 2018) with the 'plspm' package (Sanchez et al. 2017).

Results:

Godwit densities ranged from 0 – 1,436 individuals per km, with a mean of 178 ± 266 individuals per km (Table I). Quetalmahue-Puente had the highest average godwit density (n = 633 ± 210 individuals per km; Table I). We failed to detect godwits at six bays, including two bays with historically high numbers (Putemún and Rilán) despite making repeated trips to both

(n = 4 trips each; Table I).

Most bays varied considerably in both risks and rewards (Table VI). Levels of alertness and agitation for individuals varied among bays. Caulín had the highest levels of perceived disturbances, averaging 6.9 ± 6.3 flushes per survey and even reaching 18 flushes on one occasion (29 February 2016). Godwits scanned (alert/vigilant per minute) the most at Chacao (μ = 3.6 ± 4.2 times per minute; Table II). While individuals at Chamiza-Norte probed at higher rates (μ = 32.8 ± 0 times per minute; Table I), Astillero had the highest average foraging success rate (μ = 0.5 ± 0.2 items per minute; Table I).

Our fitted PLS-PM (GoF = 0.37) identified three of our predictors – foraging success, amount of intertidal foraging habitat, and alertness and agitation – as directly affecting godwit density (Figure 4, Table VII). These three latent variables explained more than three-quarters of the total effects on godwit density (Table VIII). In turn, high godwit density was significantly associated with increased godwit body condition (Figure 4, Table VIII).

Direct paths comprised 80% of the total effect on godwit density compared to 20% for indirect paths (Table VIII). However, the direct path comprised only 41% of the total effect on godwit body condition compared to 59% for indirect paths (Table VIII). Godwits aggregated into denser flocks that were in better body condition at bays where individuals had higher foraging success rates (Figure 4, Table VIII). However, disturbances resulting in displacement flights and higher levels of alertness reduced flocks densities and godwit body condition (Figure 4, Table VIII). The amount of intertidal foraging habitat also had a strong total effect on increasing both density and body condition of godwits (Table VIII). Overall, in bays with individuals in better than average condition, individuals were 35% less alert and agitated, had access to 77% more foraging habitat, experienced 61% more foraging success, and occurred in 17% larger flock

densities than in those bays in which individuals were in below average condition.

Alertness and agitation had a larger effect on both density and body condition of godwits than did the combined total effect of foraging success and amount of intertidal habitat (godwit density: 0.49, body condition: 0.17; Table VIII). However, foraging habitat factors had a greater effect on both density and body condition than did the combined individual effects of our direct measurements of human disturbances and predation risk (godwit density: 0.30, body condition: 0.10).

Discussion:

Patch quality, as measured by density and body condition of Hudsonian Godwits in the Chiloé Island region of southern Chile, was primarily driven by increased availability of suitable foraging substrate, better foraging success, and less disturbance or perceived risk (i.e., as indicated by alertness and agitation). In general, flock density increased with foraging success and available substrate, and godwits in more dense flocks were in better body condition. Collectively these patterns suggest that density may be a suitable indicator of patch quality. Though we detected no strong signal from specific agents of disturbance (i.e., numbers of humans, dogs, hoofed animals, boats, and predators), responses of godwits to those disturbances (alertness and agitation) negatively impacted flock density and body condition. Human disturbances and predation risk may thus influence foraging patch decisions and reduce godwit densities through induced changes in foraging behaviors.

Foraging shorebirds must cope with constantly changing resource availability inherent within the tidal cycle. Many species of shorebirds are highly mobile and move among many foraging patches in response to spatial or temporal changes in resources (Brown 1999, van Gils

et al. 2003). Habitat selection ultimately should reflect both the potential rewards and risks at a particular patch, though not all individuals may be able to optimize decisions and hence still occur at risky or low quality sites. For example, younger birds or those in poor condition are more likely to forage in risky areas (Cresswell 1994b, Duijns et al. 2009, Cresswell et al. 2010). We suspect that this was the case at sites like Chacao, which had high levels of disturbance and where godwits were in poor body condition. Shorebirds foraging at risky sites can use a variety of anti-predator behaviors to mitigate the riskiness of their chosen habitats, including increasing flock size to reduce danger and decreasing time spent feeding to increase vigilance rates (Cresswell 1994a, Whitfield 2003, Lind and Cresswell 2005). Alternatively, individuals can balance the benefits of foraging with the costs of predation by using less profitable sites if they avoid predators or human disturbance (Cresswell and Whitfield 1994, Ydenberg et al. 2002, Yasué et al. 2003). Accordingly, in our study, godwits were less numerous and in poorer condition in bays where they were more alert and agitated, and these behaviors predicted density better than did foraging success and amount of intertidal habitat. Alarmingly, we failed to detect any godwits using two historically important sites (Putemún and Rilán). Putemún previously hosted as many as 7,000 godwits (Andres et al. 2009), yet we detected zero godwits across four visits. Instead, Putemún was our second highest site in terms of human impact with as many as 24 people harvesting kelp and mussels at the tideline. Thus, foraging godwits may prioritize avoiding risky patches unless necessary due to individual condition.

In addition to avoiding risky sites, we found that godwits aggregated at sites where individuals had higher foraging success rates and where more suitable foraging habitat was available. The distribution of foraging shorebirds is often directly correlated with the density of their main prey, and this relationship occurs spatially at both large (e.g., between-mudflats:

Goss-Custard 1970, Finn et al. 2008, Schlacher et al. 2014) and small scales (e.g., within-mudflat: Colwell and Landrum 1993, Ribeiro et al. 2004, Pomeroy 2006). While the distribution and availability of preferred prey for godwits in the Chiloé Island region are unknown, the strong effect of foraging success suggests heterogeneity in prey distribution or density among bays. However, foraging substrate may be as important as prey density for foraging godwits. For instance, Dunlin (*Calidris alpina*) foraging in wet substrates target different prey species, resulting in individuals obtaining 40% more energy intake than individuals foraging in dry substrates (Santos et al. 2010). Thus, foraging substrates may vary in terms of invertebrate communities, prey densities, and capture efficiencies (Senner and Coddington 2011). Because foraging success and foraging substrate were both related to godwit densities and body condition in our study, further exploration of the availability of prey communities at each bay is required to fully understand patch quality for godwits.

Although not associated with direct effects, the perceived responses to human disturbances and predators (scanning behaviors and displacement flights) were negatively related to density and body condition of godwits. Peregrine Falcons are relatively uncommon in the Chiloé region (detected at only 5 of 42 bays), which may explain the lack of a direct influence predation risk on foraging patch decisions for godwits. However, the combined effect of predation risk and human activity may affect godwits through non-lethal effects. Many studies of human disturbance and predation focus only on the displacement of shorebirds from feeding areas or on lethal effects of predation rather than on less obvious and more difficult to measure behavioral changes (Burger 1981, Yasué 2005). In cases where there are few alternative foraging habitats nearby, shorebirds may change their behaviors in response to disturbances but may not be displaced. Non-lethal effects of disturbance or predation can reduce foraging rates, increase

scanning behaviors, and ultimately, affect an individual's fitness (Goss-Custard et al. 2006, Cresswell 2008). Such reduced consumption may force individuals to use riskier sites, forage for longer periods of time, and, ultimately, impair their ability to accumulate fuel reserves for migration. Not only may the cumulative impacts from many small-scale disturbances equal or exceed that of large-scale disturbances, but even minimal reductions in foraging time may be meaningful when they accumulate over tidal cycles, weeks, or months (West et al. 2002, Goss-Custard et al. 2006). Moreover, disturbances that displace individuals from one site to another might compromise non-displaced individuals at the "new" site via density-dependent effects (Burton et al. 2006, Rutten et al. 2010). Thus, subtle behavioral changes may negatively affect godwits by reducing foraging time due to increased rates of alertness and agitation, which may alter pre-migratory fueling and condition of individuals.

The association between patch quality and body condition can have implications for the ability of godwits to prepare for their migrations. Shorebirds undertake some of the most extreme migrations of any species (Gill et al. 2009, Senner et al. 2014, Conklin et al. 2017), and pre-migratory fueling plays a critical role in an individual's ability to complete migration. In order to do so, some species double their weight either prior to migration or at key stopover sites (Kvist and Lindström 2003, Piersma et al. 2005), and many rely on high intake rates to rapidly increase their body mass and condition (Piersma et al. 2005, Duijns et al. 2009). Abrupt changes in migratory fueling rates have been linked to catastrophic population declines (e.g., *rufa* Red Knots using Delaware Bay, USA; Baker et al. 2004). In the Chiloé region, godwit body condition improved with foraging success and amounts of intertidal habitat and declined as alertness and agitation rose. Body condition on the non-breeding grounds has also been linked with reproductive success through reversible state effects (Harrison et al. 2011, Senner et al.

2015). In particular, individuals in better condition arrive at the breeding grounds earlier, which may promote survival and reproductive success (Marra et al. 1998, Duijns et al. 2017). Thus, the quality of foraging sites in the Chiloé region may have far-reaching consequences for godwit population dynamics.

Our study provides evidence that the distribution and body condition of Hudsonian Godwits on the non-breeding grounds in the Chiloé Island region is strongly affected by levels of alertness and agitation of individuals and by the foraging potential of tidal mudflats. While foraging success and amount of foraging habitat were positively associated with godwit densities and body condition, behavioral responses (increased alertness and displacement flights) to perceived threats had a stronger negative influence on godwit densities and body condition. Based on these findings, we suggest that human activities that disturb shorebirds, such as humans or dogs at or near the tideline, should be minimized at bays with large flocks of foraging godwits. Easy and quick assessments of densities and relative body condition of the foraging flock may be able to aid conservation practitioners on selecting sites to implement management or to conserve. Furthermore, given the recent declines experienced by godwits, the impact of patch quality on the non-breeding grounds requires further in-depth study to assess the consequences for foraging godwits and any potential long-term effects reduced body condition may have.

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TABLES AND FIGURES

Table I. Mean and standard deviation (sd) for the number of visits, body condition, godwit densities, foraging success, and amount of intertidal foraging habitat at each bay surveyed in the Chiloé Island, Chile region. Bays where no Hudsonian Godwits (*Limosa haemastica*) were ever seen have dashes (-) for body condition and foraging success variables.

		Body Condition				Godwit Density		Foraging Success								Intertidal Habitat	
	Num of Visits	Body Molt Score		Abdominal Profile Index		Flock size per km		Probes per minute		Success Rate		Swallows per minute		Success rate per minute		% Mud and Algae	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Achao	4	2.2	0.6	3.0	0.0	117.8	95.4	14.4	10.0	0.1	0.1	1.7	1.1	0.0	0.0	85.8	7.8
Aldachildo	2	2.7	0.5	3.5	0.7	33.7	2.8	16.8	0.0	0.1	0.0	1.6	0.0	0.0	0.0	6.3	5.3
Ancud	4	0.7	0.5	3.1	0.3	18.3	10.2	25.6	6.6	0.3	0.1	6.4	2.4	0.1	0.0	10.0	0.0
Astillero	3	2.2	0.4	3.0	0.0	177.4	109.8	27.6	10.3	0.5	0.2	15.3	12.6	0.1	0.0	82.5	17.5
Aucar	4	0.7	0.4	3.0	0.0	25.3	34.4	14.1	9.7	0.1	0.1	2.4	2.7	0.0	0.0	15.0	0.0
Calén	3	1.4	0.0	3.0	0.0	29.8	51.5	6.4	11.0	0.0	0.1	0.7	1.3	0.0	0.0	26.3	26.3
Caulín	7	1.2	1.0	3.0	0.0	466.3	147.8	23.7	1.5	0.3	0.1	6.3	1.5	0.1	0.0	93.9	1.5
Chacao	2	0.8	1.1	3.0	0.0	30.9	33.9	16.9	17.3	0.2	0.2	5.7	7.8	0.0	0.0	13.3	0.0
Chamiza-Norte	1	3.3	0.0	4.0	0.0	104.2	0.0	32.8	0.0	0.2	0.0	7.4	0.0	0.1	0.0	100.0	0.0
Chamiza-Sur	4	2.0	1.5	3.5	0.6	491.4	552.6	24.1	5.7	0.2	0.0	3.5	0.4	0.0	0.0	82.5	8.2
Chúllec	7	0.6	0.4	3.0	0.0	345.9	463.9	8.8	12.1	0.1	0.1	2.6	3.6	0.0	0.0	89.3	1.9
Compu	3	2.5	0.6	3.5	0.7	80.5	70.1	17.2	15.0	0.2	0.2	6.4	5.8	0.0	0.0	37.5	10.0
Contuy	3	2.3	0.5	3.0	0.0	90.7	80.4	14.5	12.6	0.2	0.1	3.4	3.0	0.0	0.0	96.7	4.7
Contuy-Oeste	3	2.6	0.0	4.0	0.0	166.7	184.4	22.7	0.0	0.3	0.0	6.4	0.0	0.1	0.0	60.0	0.0
Curaco de Vélez	7	1.5	1.0	3.0	0.0	333.8	539.9	14.2	11.4	0.2	0.2	3.7	3.0	0.1	0.1	97.9	1.5
Huapilacuy	2	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	55.0	0.0
Huelden	2	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	5.0	0.0
Huildad	1	0.5	0.0	3.0	0.0	466.7	0.0	21.4	0.0	0.1	0.0	2.6	0.0	0.0	0.0	100.0	0.0
Ichuac	2	2.3	0.0	3.0	0.0	8.4	11.9	9.4	13.3	0.1	0.2	2.4	3.4	0.1	0.1	75.0	21.2
Lenca	2	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	10.0	0.0
Linao	4	1.0	0.7	3.3	0.5	53.1	26.9	17.5	3.2	0.2	0.0	3.2	0.6	0.1	0.0	19.2	2.0
Llicaldad	3	1.1	1.4	3.0	0.0	30.3	31.7	21.4	0.1	0.2	0.0	3.3	0.5	0.0	0.0	85.0	0.0
Llicaldad-Sur	2	1.9	0.0	3.0	0.0	193.6	273.8	7.5	10.6	0.1	0.1	1.5	2.1	0.0	0.0	36.3	8.8

TABLE I (CONTINUED)

		Body Condition				Godwit Density		Foraging Success								Intertidal Habitat	
	Num of Visits	Body Molt Score		Abdominal Profile Index		Flock size per km		Probes per minute		Success Rate		Swallows per minute		Success rate per minute		% Mud and Algae	
		Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Manao	3	1.3	1.0	3.0	0.0	141.0	142.7	21.4	1.3	0.1	0.1	2.2	1.7	0.0	0.0	69.3	3.3
Nercón	6	0.9	0.6	3.0	0.0	222.8	188.4	19.2	12.2	0.1	0.1	3.3	2.2	0.0	0.0	89.3	0.0
Nercón-Puente	4	1.3	0.7	3.0	0.0	323.2	345.4	26.7	2.4	0.3	0.3	8.6	7.5	0.1	0.1	88.3	0.0
Piluco	3	1.0	0.0	3.0	0.0	101.4	77.4	23.1	0.0	0.2	0.0	4.7	0.0	0.0	0.0	25.0	0.0
Pullao	5	1.6	1.0	3.0	0.0	318.4	248.3	20.9	2.4	0.3	0.1	5.7	3.1	0.1	0.0	91.5	10.7
Pullihue-Puente	2	0.0	0.0	3.0	0.0	0.3	0.4	9.5	13.4	0.2	0.3	3.5	4.9	0.0	0.0	90.0	0.0
Putemún	4	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	68.1	8.8
Quellón	2	0.6	0.0	3.0	0.0	196.3	68.1	27.6	0.0	0.2	0.0	6.3	0.0	0.1	0.0	90.0	0.0
Quetalco	2	0.7	0.4	3.0	0.0	67.8	34.6	25.2	3.1	0.2	0.0	4.3	0.9	0.0	0.0	71.7	0.0
Quetalmahue-Este	3	0.6	0.6	3.0	0.0	37.3	27.3	6.5	1.0	0.1	0.0	0.4	0.2	0.0	0.0	45.0	0.0
Quetalmahue-Oeste	5	1.4	1.6	3.0	0.0	116.3	197.6	12.5	14.5	0.1	0.2	3.0	3.5	0.0	0.0	96.7	0.0
Quetalmahue-Puente	6	1.0	1.0	2.6	0.9	632.6	209.6	26.7	4.4	0.3	0.0	8.3	2.0	0.1	0.1	83.3	0.0
Quillaipe	2	2.5	0.0	3.0	0.0	37.8	53.5	9.9	14.1	0.1	0.1	1.3	1.8	0.0	0.0	78.3	0.0
Quinchao	2	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	80.0	0.0
Rilán	4	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	90.0	0.0
San Juan	5	1.3	0.8	3.0	0.0	231.8	222.4	20.4	4.2	0.1	0.0	2.9	0.7	0.0	0.0	74.4	30.4
Teguel	3	1.7	1.4	3.0	0.0	270.6	259.4	17.4	2.1	0.2	0.0	3.9	0.9	0.0	0.0	72.3	5.3
Ten Ten	9	1.2	1.2	3.0	0.0	28.7	45.2	7.7	10.8	0.1	0.1	1.9	3.5	0.0	0.0	95.0	2.5
Yaldad	2	2.3	0.0	3.0	0.0	128.2	67.4	12.9	0.0	0.1	0.0	0.7	0.0	0.0	0.0	85.0	0.0
Overall	3.5	1.4	1	3.1	0.3	178.2	266.1	15	11	0.1	0.1	3.5	3.7	0.04	0.04	70.7	30.3

Table II. Mean and standard deviation (sd) for alertness and agitation, human disturbances, and predation risk at each bay surveyed in the Chiloé Island, Chile region. Bays where no Hudsonian Godwits (*Limosa haemastica*) were ever seen have dashes (-) for alertness and agitation.

	Alertness and Agitation				Human Disturbances								Predation Risk			
	Number of Flushes		Alert per minute		Number of Humans		Number of Dogs		Number of Hoofed Animals		Number of Boats		Number of Predators		Number of Predator Species	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Achao	5.0	5.6	0.3	0.4	11.3	8.1	1.9	0.1	0.0	0.0	0.4	0.4	1.0	1.4	0.5	0.6
Aldachildo	0.5	0.7	2.2	0.0	8.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
Ancud	1.0	0.8	1.2	1.2	2.8	1.8	1.3	0.9	0.0	0.0	3.5	4.0	0.0	0.0	0.0	0.0
Astillero	0.7	0.6	0.5	0.4	2.5	2.2	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aucar	0.0	0.0	0.5	0.5	1.7	2.0	0.4	0.8	0.0	0.0	0.1	0.3	0.5	0.6	0.5	0.6
Calén	0.7	1.2	0.4	0.8	4.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Caulín	6.9	6.3	0.8	0.9	8.6	7.3	0.4	0.4	0.3	0.3	0.1	0.3	1.1	1.3	0.9	0.9
Chacao	1.0	1.4	3.6	4.2	9.3	3.9	0.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chamiza-Norte	2.0	0.0	0.6	0.0	1.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chamiza-Sur	2.3	1.5	0.5	0.5	16.8	9.3	3.4	1.4	2.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Chúllec	2.4	4.4	0.1	0.2	1.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	2.2	1.0	1.8
Compu	1.3	2.3	0.1	0.1	0.6	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.2	0.3	0.6
Contuy	1.0	1.7	0.1	0.1	0.5	0.7	0.0	0.0	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Contuy-Oeste	1.0	1.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Curaco de Vélez	3.1	3.7	0.3	0.4	3.4	2.4	0.5	0.6	0.6	1.3	0.2	0.4	0.3	0.5	0.3	0.5
Huapilacuy	-	-	-	-	6.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Huelden	-	-	-	-	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Huildad	1.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ichuac	0.5	0.7	0.3	0.4	0.3	0.4	0.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lenca	-	-	-	-	2.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Linao	1.8	1.5	0.6	0.4	10.5	8.0	0.2	0.2	0.3	0.5	0.6	0.3	0.3	0.5	0.3	0.5
Llicaldad	1.7	1.5	2.8	3.4	9.3	1.1	1.8	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Llicaldad-Sur	0.0	0.0	0.4	0.6	13.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Manao	4.3	5.1	0.4	0.0	4.6	7.9	0.3	0.6	0.0	0.0	0.3	0.6	0.3	0.6	0.3	0.6
Nercón	1.3	1.8	0.2	0.3	7.3	6.1	1.6	1.2	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0

TABLE II (CONTINUED)

	Alertness and Agitation				Human Disturbances								Predation Risk			
	Number of Flushes		Alert per minute		Number of Humans		Number of Dogs		Number of Hoofed Animals		Number of Boats		Number of Predators		Number of Predator Species	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Nercón-Puente	0.5	0.6	0.4	0.2	5.2	2.6	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Piluco	1.0	1.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pullao	3.0	2.5	0.3	0.2	1.8	1.9	0.0	0.0	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0
Pullihue-Puente	0.0	0.0	0.4	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.7	0.5	0.7
Putemún	-	-	-	-	15.3	21.7	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quellón	1.0	1.4	0.3	0.0	2.5	0.7	0.8	1.1	0.0	0.0	0.3	0.4	0.5	0.7	0.5	0.7
Quetalco	0.5	0.7	0.3	0.4	4.0	2.1	0.0	0.0	0.5	0.7	0.8	0.4	0.0	0.0	0.0	0.0
Quetalmahue-Este	0.0	0.0	0.1	0.1	1.5	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quetalmahue-Oeste	0.6	0.9	0.4	0.5	6.1	4.0	0.1	0.2	0.8	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Quetalmahue-Puente	2.3	4.3	0.3	0.2	4.6	1.7	0.1	0.2	0.0	0.0	0.0	0.0	0.7	1.2	0.3	0.5
Quillaipe	3.0	4.2	0.6	0.8	5.0	0.0	1.5	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quinchao	-	-	-	-	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rilán	-	-	-	-	1.7	1.5	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
San Juan	1.4	1.5	0.3	0.3	4.3	3.4	0.8	1.0	0.0	0.0	0.1	0.2	0.2	0.4	0.2	0.4
Teguel	4.3	3.1	0.5	0.3	0.9	1.0	0.1	0.2	0.0	0.0	0.0	0.0	2.3	2.3	2.0	1.7
Ten Ten	0.3	0.5	0.2	0.3	4.3	3.1	0.9	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Yaldad	2.5	0.7	0.9	0.0	5.5	6.4	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0
Overall	1.7	2.9	0.5	0.9	5	5.9	0.6	0.9	0.2	0.6	0.2	0.9	0.3	0.9	0.2	0.7

Table III. Values for bay characteristics, land use, and water at each bay surveyed in the Chiloé Island, Chile region. Each variable was collected once per bay.

	Bay Characteristics			Land Use		Water		
	Tidal Area (km^2)	Bay Width (m)	Bay Perimeter (km)	Road Substrate	Distance to Road (m)	Distance to Aquaculture	Shellfish Aquaculture	Percent Aquaculture
Achao	0.4	69.8	2.0	Paved	60.0	None	No	0.0
Aldachildo	0.3	154.4	1.0	Beach	0.0	Medium	Yes	35.0
Ancud	1.0	72.4	1.7	Dirt	10.0	None	No	0.0
Astillero	0.2	331.2	1.2	Beach	0.0	None	No	0.0
Aucar	1.0	420.4	2.3	Paved	85.0	Distant	Yes	75.0
Calén	0.3	113.6	3.0	Beach	0.0	Close	Yes	30.0
Caulín	2.6	545.8	3.6	Beach	0.0	None	No	0.0
Chacao	0.3	290.9	1.9	Paved	45.0	None	No	0.0
Chamiza-Norte	1.9	635.9	5.8	Paved	200.0	None	No	0.0
Chamiza-Sur	3.0	572.6	3.0	Paved	50.0	None	No	0.0
Chúllec	0.5	299.5	2.0	Beach	0.0	Close	Yes	70.0
Compu	1.2	638.8	4.0	Beach	0.0	Medium	Yes	15.0
Contuy	2.2	1310.7	7.2	Beach	0.0	None	No	0.0
Contuy-Oeste	0.7	1857.8	4.4	Dirt	50.0	None	No	0.0
Curaco de Vélez	0.7	774.3	3.1	Paved	0.0	Distant	Yes	10.0
Huapilacuy	0.2	25.7	4.6	Beach	0.0	Close	Yes	10.0
Huelden	0.2	289.6	1.5	Dirt	20.0	Distant	Yes	0.0
Huildad	2.0	1167.3	6.0	Dirt	75.0	Distant	Yes	0.0
Ichuac	0.3	319.7	3.3	Beach	0.0	None	No	0.0
Lenca	1.5	641.6	2.3	Beach	0.0	Distant	No	1.0
Linao	0.2	204.5	5.8	Dirt	0.0	Medium	Yes	40.0
Llicaldad	0.1	90.5	1.1	Paved	90.0	Distant	Yes	10.0
Llicaldad-Sur	0.0	147.3	0.4	Paved	90.0	Distant	Yes	5.0
Manao	1.1	476.9	2.7	Dirt	35.0	Distant	Yes	5.0
Nercón	0.2	82.5	1.5	Beach	0.0	Distant	Yes	25.0

TABLE III (CONTINUED)

	Bay Characteristics			Land Use		Water		
	Tidal Area (km^2)	Bay Width (m)	Bay Perimeter (km)	Road Substrate	Distance to Road (m)	Distance to Aquaculture	Shellfish Aquaculture	Percent Aquaculture
Nercón-Puente	0.1	183.7	0.8	Paved	0.0	Distant	Yes	10.0
Piluco	0.1	38.9	1.5	Paved	0.0	None	No	0.0
Pullao	2.1	233.7	4.6	Beach	0.0	Distant	Yes	25.0
Pullihue-Puente	0.1	28.9	1.8	Paved	0.0	None	No	0.0
Putemún	3.5	829.6	9.0	Dirt	10.0	None	No	0.0
Quellón	0.3	65.6	2.7	Paved	30.0	None	No	0.0
Quetalco	0.2	262.9	1.4	Beach	0.0	Close	Yes	90.0
Quetalmahue-Este	0.1	29.6	1.1	Paved	35.0	None	No	0.0
Quetalmahue-Oeste	0.3	137.1	1.3	Paved	100.0	None	No	0.0
Quetalmahue-Puente	0.9	759.1	1.7	Beach	0.0	Close	Yes	10.0
Quillaipe	1.3	1907.9	5.8	Dirt	25.0	Medium	Yes	30.0
Quinchao	1.0	387.2	2.3	Beach	0.0	Close	Yes	60.0
Rilán	0.4	657.7	2.5	Beach	0.0	Close	Yes	40.0
San Juan	0.8	545.0	2.7	Beach	20.0	Close	Yes	60.0
Teguel	0.3	445.9	1.5	Beach	0.0	Close	Yes	50.0
Ten Ten	0.2	602.9	2.0	Paved	0.0	None	No	0.0
Yaldad	1.4	382.1	3.9	Beach	0.0	Medium	Yes	30.0
Overall	0.9	449.3	2.8	Dirt	18.9	Close to Medium	Yes	18.4

Table IV. The outer model fit of the fitted partial least squares path model. The Cronbach's alpha is a coefficient that is intended to evaluate how well a block of indicators measures their corresponding latent construct with values greater than 0.7 considered acceptable. The Dillon-Goldstein's rho focuses on the variance of the sum of variables in the block of interest, with a block considered as unidimensional when the Dillon-Goldstein's rho is larger than 0.7. Lastly, if a block is unidimensional, the first eigenvalue should be "much more" larger than 1, whereas the second eigenvalue should be smaller than 1.

	Cronbach's alpha	Dillon-Goldstein's rho	1st Eigenvalue	2nd Eigenvalue
Foraging Success	0.93	0.95	3.32	0.41
Predation Risk	0.95	0.98	1.91	0.09
Humans	0.91	0.94	2.52	0.31
Dogs	0.81	0.89	2.21	0.67
Boats	0.99	0.98	2.96	0.03
Hoofed	0.81	0.89	2.21	0.68
Alertness and Agitation	0.84	0.92	1.72	0.28
Land Use	0.72	0.88	1.56	0.44
Water	0.80	0.89	2.17	0.71
Landscape and Bay Characteristics	0.77	0.87	2.05	0.63
Amount of Intertidal Habitat	1.00	1.00	1.00	0.00
Godwit Density	1.00	1.00	1.00	0.00
Body Condition	0.89	0.95	1.81	0.19

Table V. Outer model output of the fitted partial least squares path model. Weight indicates the weighting used in the outer model. Loadings are the correlations between a latent variable and its indicators. Communalities are the squared loading values and indicate the amount of variability explained by a latent variable (e.g., for probes per minute the communality value of 0.78 (0.88^2) indicates that 78% of the variability for this variable is explained by the latent variable 'Foraging Success').

	weight	loading	communality
Foraging Success			
Probes per min	0.31	0.88	0.78
Success rate	0.28	0.97	0.94
Swallows per min	0.24	0.94	0.88
Success rate per min	0.28	0.85	0.71
Predation Risk			
Number of predator species	0.78	0.99	0.99
Number of predators	0.23	0.94	0.89
Humans			
Number of humans	0.42	0.95	0.90
Number of humans at tideline	0.44	0.94	0.89
Number of humans near godwits	0.22	0.85	0.71
Dogs			
Number of dogs	0.48	0.96	0.92
Number of dogs at tideline	0.41	0.93	0.65
Number of dogs near godwits	0.24	0.64	0.42
Boats			
Number of boats	0.32	0.99	0.99
Number of boats at tideline	0.37	0.99	0.98
Number of boats near godwits	0.36	0.99	0.99
Hoofed Animals			
Number of hoofed animals	0.29	0.91	0.83
Number of hoofed animals near tideline	1.00	0.97	0.95
Number of hoofed animals near godwits	-0.36	0.68	0.47
Alertness and Agitation			
Number of flushes per min	0.64	0.95	0.91
Number of times alert/vigilant per min	0.43	0.89	0.81
Land Use			
Distance to road	0.20	0.69	0.47
Road substrate	0.88	0.98	0.97

TABLE V (CONTINUED)

	weight	loading	communality
Water			
Distance to aquaculture	0.29	0.78	0.61
% aquaculture	0.39	0.79	0.63
Shellfish	0.47	0.96	0.92
Bay Characteristics			
Bay perimeter	0.21	0.82	0.67
Bay width	0.30	0.67	0.45
Tidal area	0.67	0.93	0.87
Amount of Intertidal Habitat			
% mud + % algae	1.00	1.00	1.00
Godwit Density			
Flock size per km	1.00	1.00	1.00
Body Condition			
Body molt score residuals	0.48	0.94	0.88
Abdominal profile index residuals	0.57	0.96	0.92

Table VI. Average standardized latent variable scores of each tidal mudflat surveyed. Only latent variables with significant relationships with density and body condition of Hudsonian Godwits (*Limosa haemastica*) are shown.

	Body Condition	Godwit Density	Alertness and Agitation	Amount of Intertidal Habitat	Foraging Success
Achao	0.40	-0.23	0.24	0.50	-0.37
Aldachildo	1.15	-0.55	0.53	-2.14	-0.13
Ancud	0.53	-0.60	1.16	-2.01	0.88
Astillero	0.86	0.00	0.52	0.39	1.58
Aucar	0.21	-0.58	0.24	-1.85	-0.23
Calén	-0.75	-0.56	0.22	-1.48	-0.90
Caulín	0.41	1.09	-1.94	0.77	0.74
Chacao	0.62	-0.56	1.51	-1.90	0.37
Chamiza-Norte	1.59	-0.28	-0.04	0.97	1.12
Chamiza-Sur	1.08	1.18	-1.03	0.39	0.28
Chúllec	-0.98	0.63	-0.16	0.62	-0.34
Compu	0.48	-0.37	0.10	-1.10	0.54
Contuy	-0.01	-0.33	-0.05	0.86	0.07
Contuy-Oeste	-0.64	-0.04	0.32	-0.36	0.33
Curaco de Vélez	-0.16	0.59	-0.91	0.90	0.18
Huapilacuy	-1.15	-0.67	0.12	-0.52	-1.31
Huelden	-1.18	-0.67	0.12	-2.18	-1.31
Huildad	0.55	1.09	-1.63	0.97	-0.04
Ichuac	-0.49	-0.64	0.34	0.14	-0.16
Lenca	-1.43	-0.67	0.12	-2.01	-1.31
Linao	0.67	-0.47	0.20	-1.71	0.21
Llicaldad	0.73	-0.56	1.23	0.47	0.14
Llicaldad-Sur	-0.37	0.06	0.21	-1.14	-0.74
Manao	0.72	-0.14	-0.08	-0.05	-0.05
Nercón	0.04	0.17	0.05	0.62	0.00
Nercón-Puente	0.23	0.55	0.07	0.58	0.70
Piluco	-0.28	-0.29	0.71	-1.52	0.16
Pullao	0.33	0.53	-0.44	0.69	0.61
Pullihue-Puente	-0.58	-0.67	0.24	0.64	-0.10
Putemún	-1.00	-0.67	0.12	-0.09	-1.31
Quellón	-0.44	0.07	0.02	0.64	0.45
Quetalco	0.44	-0.42	0.29	0.03	0.42
Quetalmahue-Este	0.60	-0.53	0.12	-0.85	-0.56
Quetalmahue-Oeste	-0.35	-0.23	0.18	0.86	-0.20
Quetalmahue-Puente	0.19	1.71	-0.20	0.42	1.21
Quillaipe	-0.13	-0.53	0.15	0.25	-0.56
Quinchao	-1.14	-0.67	0.12	0.31	-1.31
Rilán	-1.02	-0.67	0.12	0.64	-1.31
San Juan	0.17	0.20	-0.07	0.12	0.08

TABLE VI (CONTINUED)

	Body Condition	Godwit Density	Alertness and Agitation	Amount of Intertidal Habitat	Foraging Success
Teguel	0.73	0.35	0.10	0.05	0.27
Ten Ten	-0.18	-0.56	0.40	0.80	-0.34
Yaldad	0.04	-0.19	0.07	0.47	-0.34

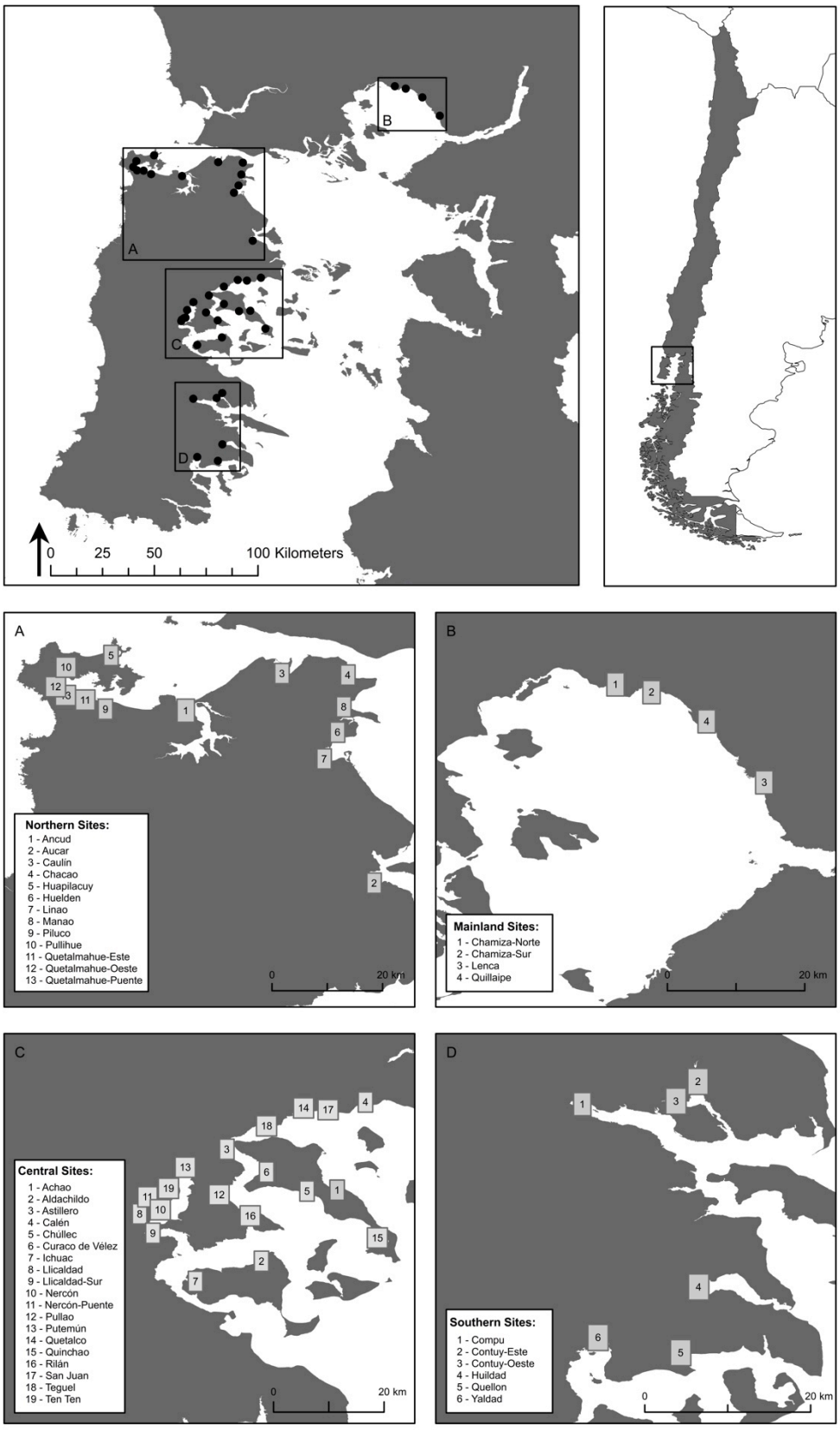
Table VII. Results of bootstrapping procedure of the fitted partial least squares path model. Significant paths, where 95% confidence intervals (CI) did not cross 0, are in bold.

	Beta	95% CI
Foraging Success -> Godwit Density	**0.34**	**(0.23, 0.47)**
Predation Risk -> Alertness and Agitation	0.02	(-0.15, 0.06)
Predation Risk -> Godwit Density	0.01	(-0.07, 0.16)
Humans -> Alertness and Agitation	**0.15**	**(0.04, 0.31)**
Dogs -> Alertness and Agitation	0.06	(-0.30, 0.45)
Boats -> Alertness and Agitation	0.12	(-0.15, 0.39)
Hoofed Animals -> Alertness and Agitation	-0.06	(-0.24, 0.07)
Humans -> Godwit Density	-0.01	(-0.13, 0.14)
Dogs -> Godwit Density	-0.02	(-0.22, 0.21)
Boats -> Godwit Density	-0.01	(-0.15, 0.39)
Hoofed Animals -> Godwit Density	-0.03	(-0.12, 0.08)
Alertness and Agitation -> Godwit Density	**-0.57**	**(-0.75, -0.35)**
Land Use -> Bay Characteristics	0.23	(-0.30, 0.44)
Water -> Bay Characteristics	**-0.30**	**(-0.45, -0.14)**
Bay Characteristics -> Godwit Density	-0.06	(-0.16, 0.04)
Amount of Intertidal Habitat -> Foraging Success	0.11	(-0.07, 0.28)
Amount of Intertidal Habitat -> Godwit Density	**0.11**	**(0.01, 0.21)**
Godwit Density -> Body Condition	**0.34**	**(0.23, 0.44)**

Table VIII. The relative contribution of direct and indirect effects (calculated from standardized path coefficients), the total effect, and bootstrapped 95% confidence intervals for each path in the fitted partial least squares path model. Paths connect latent variables. Paths where the 95% confidence interval (CI) do not overlap zero are bolded.

	direct	indirect	total	95% CI
Land Use -> Bay Size	0.26	0.00	0.23	(-0.29, 0.43)
Land Use -> Godwit Density	0.00	-0.01	-0.01	(-0.05, 0.03)
Land Use -> Body Condition	0.00	0.00	0.00	(-0.02, 0.01)
Water -> Bay Size	**-0.29**	**0.00**	**-0.29**	**(-0.44, -0.14)**
Water -> Godwit Density	0.00	0.02	0.02	(-0.01, 0.05)
Water -> Body Condition	**0.00**	**0.01**	**0.01**	**(0.00, 0.02)**
Bay Size -> Godwit Density	-0.05	0.00	-0.06	(-0.16, 0.05)
Bay Size -> Body Condition	0.00	-0.02	-0.02	(-0.06, 0.02)
Amount of Intertidal Habitat -> Foraging Success	0.11	0.00	0.11	(-0.05, 0.25)
Amount of Intertidal Habitat -> Godwit Density	**0.10**	**0.04**	**0.14**	**(0.04, 0.24)**
Amount of Intertidal Habitat -> Body Condition	**0.00**	**0.04**	**0.05**	**(0.01, 0.09)**
Foraging Success -> Godwit Density	**0.35**	**0.00**	**0.35**	**(0.23, 0.48)**
Foraging Success -> Body Condition	**0.00**	**0.11**	**0.12**	**(0.07, 0.19)**
Predation -> Alertness and Agitation	0.00	0.00	-0.03	(-0.17, 0.1)
Predation -> Godwit Density	0.07	0.00	0.07	(-0.13, 0.25)
Predation -> Body Condition	0.00	0.02	0.02	(-0.04, 0.09)
Humans -> Alertness and Agitation	**0.15**	**0.00**	**0.15**	**(0.02, 0.29)**
Humans -> Godwit Density	-0.02	-0.09	-0.09	(-0.19, 0.04)
Humans -> Body Condition	0.00	-0.04	-0.03	(-0.07, 0.01)
Dogs -> Alertness and Agitation	0.03	0.00	0.06	(-0.34, 0.42)
Dogs -> Godwit Density	0.00	-0.02	-0.05	(-0.29, 0.31)
Dogs -> Body Condition	0.00	-0.01	-0.02	(-0.1, 0.11)
Boats -> Alertness and Agitation	0.13	0.00	0.12	(-0.16, 0.42)
Boats -> Godwit Density	0.01	-0.07	-0.08	(-0.32, 0.12)
Boats -> Body Condition	0.00	-0.02	-0.03	(-0.11, 0.04)
Hoofed Animals -> Alertness and Agitation	-0.06	0.00	-0.06	(-0.25, 0.07)
Hoofed Animals -> Godwit Density	0.00	0.04	0.01	(-0.13, 0.21)
Hoofed Animals -> Body Condition	0.00	0.01	0.00	(-0.04, 0.07)
Alertness and Agitation -> Godwit Density	**-0.59**	**0.00**	**-0.58**	**(-0.76, -0.36)**
Alertness and Agitation -> Body Condition	**0.00**	**-0.19**	**-0.19**	**(-0.28, -0.11)**
Godwit Density -> Body Condition	**0.33**	**0.00**	**0.33**	**(0.24, 0.43)**

Figure 1. Map of Chile (gray) and South America (outlined, right panel). Locations of surveyed intertidal mudflats on Chiloé Island, mainland, and adjacent islands are indicated by black circles (left panel). Panel (A) shows mudflat locations in the northern region, (B) on the mainland, (C) in the central region, and (D) in the southern region of Chiloé Island.


A
B
C
D
0 25 50 100 Kilometers
Northern Sites:
1 - Ancud
2 - Aucar
3 - Caulín
4 - Chacao
5 - Huapilacuy
6 - Huelden
7 - Linao
8 - Manao
9 - Piluco
10 - Pullihue
11 - Quetalmahue-Este
12 - Quetalmahue-Oeste
13 - Quetalmahue-Puente
0 20 km
Mainland Sites:
1 - Chamiza-Norte
2 - Chamiza-Sur
3 - Lenca
4 - Quillaipe
0 20 km
Central Sites:
1 - Achao
2 - Aldachildo
3 - Astillero
4 - Calén
5 - Chüllec
6 - Curaco de Vélez
7 - Ichuac
8 - Llicaldad
9 - Llicaldad-Sur
10 - Nercón
11 - Nercón-Puente
12 - Pullao
13 - Putemún
14 - Quetalco
15 - Quinchao
16 - Rilán
17 - San Juan
18 - Teguel
19 - Ten Ten
0 20 km
Southern Sites:
1 - Compu
2 - Contuy-Este
3 - Contuy-Oeste
4 - Huildad
5 - Quellon
6 - Yaldad
0 20 km

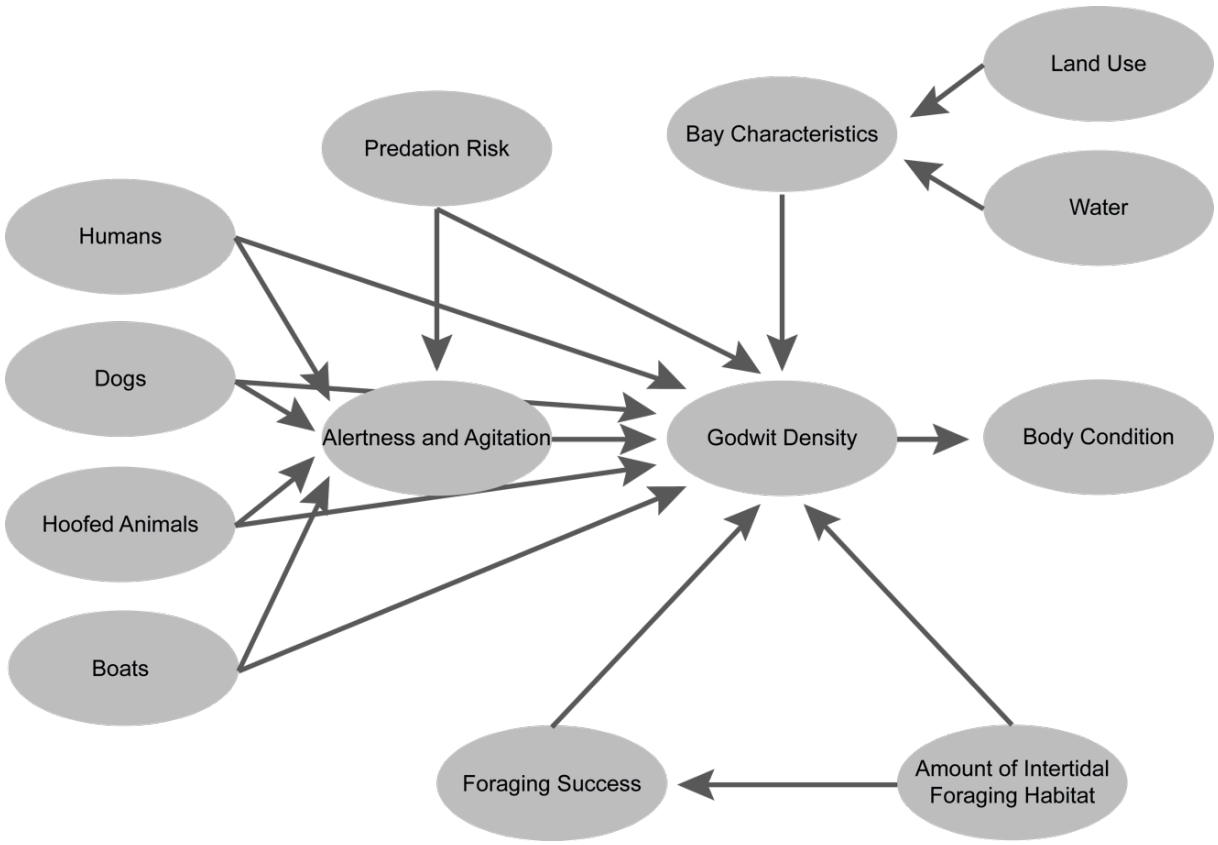


Figure 2. The partial least squares inner path model. Ovals represent each of the 'latent' variables with the proposed relationships between each latent variable shown by the dark gray arrows.

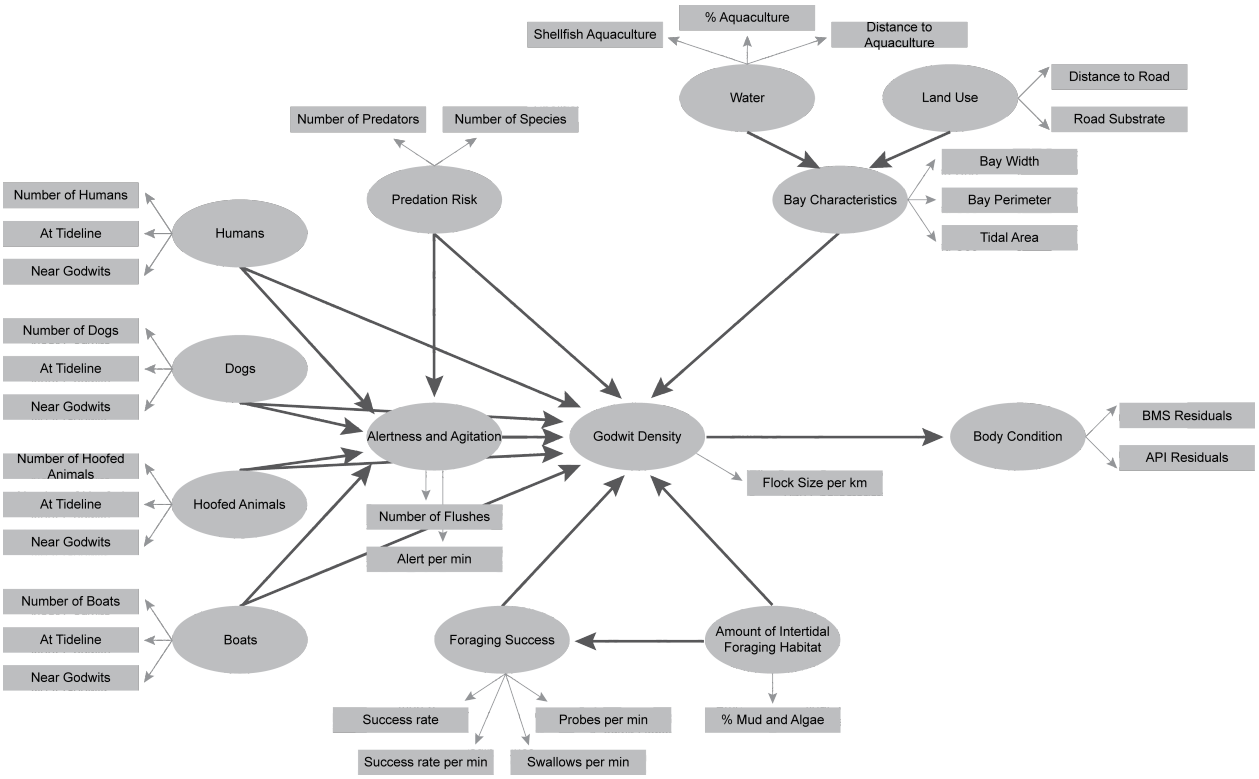


Figure 3. The final partial least squares path model. 'Manifest' variables are shown in rectangles and 'latent' variables in ovals. The light gray arrows show the link between the manifest variables and each latent variable. The inner model describing the relationships between the latent variables is represented using dark gray arrows.

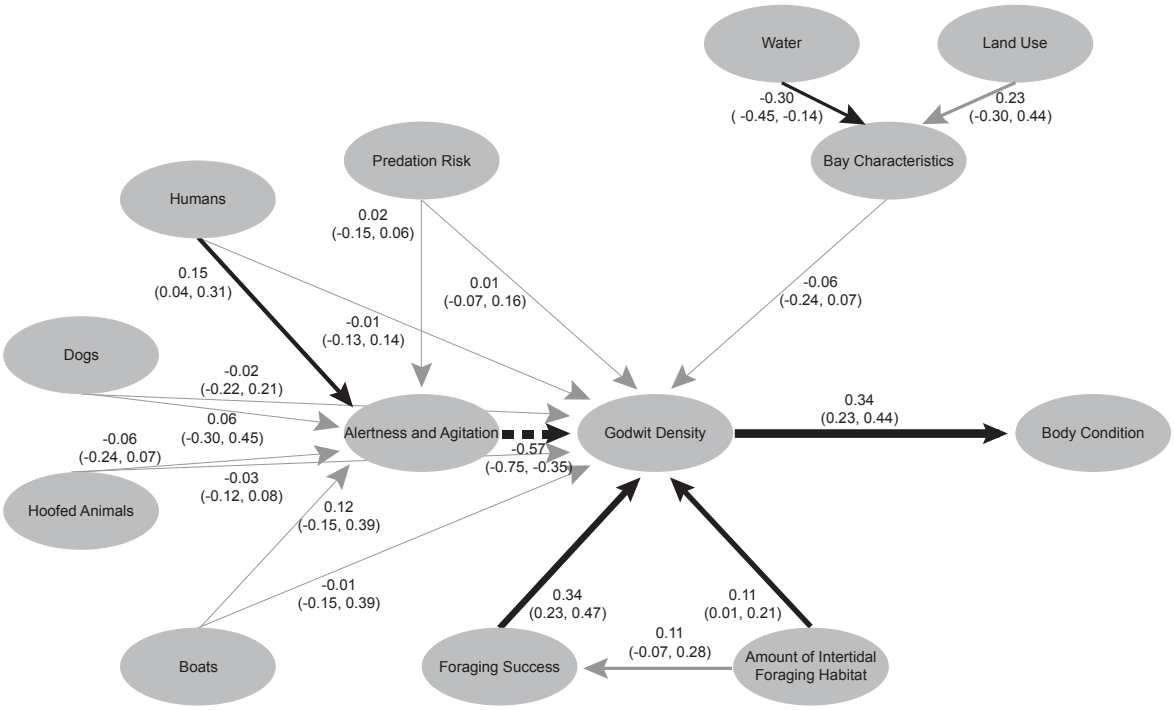


Figure 4. Partial least squares path diagram used to assess both direct and indirect effects on density and body condition of Hudsonian Godwits (*Limosa haemastica*) in the Chiloé Island region. Arrows point from predictor to response variables within the model and the thickness of the arrows is proportional to the respective path values (mean bootstrapped standardized path coefficients). Black lines represent significant relationships while gray lines represent non-significant relationships based on 999 bootstrapped iterations. For significant relationships, solid lines represent positive relationships, while dashed lines represent negative relationships. Coefficients of determination (R^2) and 95% confidence intervals are reported for response variables within the model.

APPENDIX D

Table DI. Survey data of non-breeding season patch quality, foraging success, intertidal foraging habitat, predation risk, and alertness and agitation of Hudsonian Godwits (*Limosa haemastica*) on Chiloé Island, Chile in 2016. When no godwits were seen body molt score, abdominal profile index, probes per min, success rate, success rate per min, number of flushes, and alertness per minute have a (-).

Date	Location	Flock size per km	Length of Survey (min)	Body Molt Score	Abdominal Profile Index	Probes per min	Success Rate	Swallows per min	Success Rate per min	% Mud and Algae	Number of Predators	Number of Predator Species	Number of Flushes	Alert per min
Jan 02	Chacao	7	40	0.00	3.00	4.68	0.03	0.18	0.01	13.33	0	0	2.00	6.60
Jan 03	Aucar	0	65	0.00	0.00	0.00	0.00	0.00	0.00	15.00	1	1	0.00	0.00
Jan 03	Ancud	22	40	0.00	3.00	21.33	0.13	2.79	0.03	10.00	0	0	1.00	2.90
Jan 04	Caulín	429	350	0.30	3.00	24.63	0.30	7.60	0.06	93.94	3	2	10.00	1.07
Jan 05	Quetalmahue-Oeste	0	50	-	-	-	-	-	-	96.67	0	0	-	-
Jan 05	Quetalmahue-Puente	636	50	0.30	3.00	NA	NA	NA	NA	83.33	0	0	0.00	NA
Jan 05	Quetalmahue-Harbor	65	10	0.20	3.00	7.14	0.08	0.58	0.02	45.00	0	0	0.00	0.00
Jan 05	Piluco	169	5	0.00	0.00	NA	NA	NA	NA	25.00	0	0	1.00	NA
Jan 06	Quetalmahue-Puente	311	120	0.20	3.00	30.01	0.33	10.02	0.08	83.33	0	0	1.00	0.00
Jan 06	Quetalmahue-Oeste	89	80	0.20	3.00	26.68	0.20	5.58	0.04	96.67	0	0	1.00	0.99
Jan 06	Quetalmahue-Este	35	7	0.20	3.00	NA	NA	NA	NA	45.00	0	0	0.00	NA
Jan 06	Piluco	17	5	0.00	0.00	NA	NA	NA	NA	25.00	0	0	0.00	NA
Jan 07	Linao	82	235	0.20	3.00	15.20	0.15	2.43	0.04	19.17	1	1	3.00	0.24
Jan 08	Manao	16	125	0.30	3.00	20.37	0.02	0.30	0.00	69.25	1	1	0.00	0.40
Jan 08	Caulín	425	180	0.30	3.00	22.89	0.25	6.34	0.06	93.94	0	0	1.00	0.03
Jan 09	Aucar	16	135	0.30	3.00	19.05	0.09	1.72	0.02	15.00	0	0	0.00	0.26
Jan 09	Ten Ten	37	15	0.30	3.00	NA	NA	NA	NA	95.00	0	0	1.00	NA
Jan 09	Putemún	0	15	-	-	-	-	-	-	72.50	0	0	-	-
Jan 09	Rilán	0	60	-	-	-	-	-	-	90.00	0	0	-	-
Jan 11	Putemún	0	60	-	-	-	-	-	-	72.50	0	0	-	-
Jan 11	Ten Ten	0	10	-	-	-	-	-	-	95.00	0	0	-	-
Jan 11	Nercón	400	45	0.40	3.00	18.07	0.20	5.77	0.05	89.29	0	0	1.00	0.20
Jan 11	Llicaldad	5	5	0.30	3.00	NA	NA	NA	NA	85.00	0	0	0.00	NA
Jan 11	Nercón	0	10	-	-	-	-	-	-	89.29	0	0	-	-
Jan 11	Nercón-Puente	619	30	0.50	3.00	28.42	0.49	13.93	0.13	88.33	0	0	1.00	0.27
Jan 11	Nercón	196	30	0.40	3.00	26.46	0.09	2.68	0.02	89.29	0	0	0.00	0.00
Jan 11	Llicaldad	66	25	0.30	3.00	21.35	0.14	2.98	0.03	85.00	0	0	3.00	5.16
Jan 12	Pullao	571	285	0.60	3.00	21.35	0.14	2.98	0.03	96.25	0	0	3.00	0.10
Jan 13	Ten Ten	5	35	0.30	3.00	22.44	0.25	8.11	0.11	95.00	0	0	1.00	0.20
Jan 13	Rilán	0	65	-	-	-	-	-	-	90.00	0	0	-	-
Jan 13	Putemún	0	5	-	-	-	-	-	-	72.50	0	0	-	-
Jan 14	Ten Ten	89	15	0.50	3.00	NA	NA	NA	NA	95.00	0	0	0.00	NA
Jan 14	Curaco de Vélez	1435	335	0.60	3.00	21.70	0.20	4.36	0.02	97.92	0	0	7.00	1.08

TABLE DI (CONTINUED)

Date	Location	Flock size per km	Length of Survey (min)	Body Molt Score	Abdominal Profile Index	Probes per min	Success Rate	Swallows per min	Success Rate per min	% Mud and Algae	Number of Predators	Number of Predator Species	Number of Flushes	Alert per min
Jan 15	Chúllec	964	105	0.30	3.00	23.57	0.20	6.07	0.04	90.00	0	0	1.00	0.15
Jan 15	Quinchao	0	15	-	-	-	-	-	-	80.00	0	0	-	-
Jan 15	Achao	0	5	-	-	-	-	-	-	85.78	0	0	-	-
Jan 15	Curaco de Vélez	0	5	-	-	-	-	-	-	97.92	0	0	-	-
Jan 16	Compu	0	10	-	-	-	-	-	-	37.50	0	0	-	-
Jan 16	Huildad	467	60	0.50	3.00	21.40	0.12	2.64	0.02	100.00	0	0	1.00	0.26
Jan 16	Quellón	244	115	0.60	3.00	27.63	0.24	6.34	0.05	90.00	1	1	2.00	0.33
Jan 17	Yaldad	176	75	0.00	0.00	NA	NA	NA	NA	85.00	1	1	3.00	NA
Jan 18	Teguel	5	40	0.10	3.00	19.64	0.22	4.96	0.04	71.50	1	1	1.00	0.89
Jan 18	Quetalco	92	70	0.40	3.00	23.05	0.16	3.70	0.03	71.67	0	0	0.00	0.00
Jan 18	San Juan	572	100	0.70	3.00	14.63	0.14	2.56	0.04	88.00	0	0	1.00	0.07
Jan 19	Quetalmahue-Oeste	0	5	-	-	-	-	-	-	96.67	0	0	-	-
Jan 19	Quetalmahue-Puente	485	145	0.80	3.00	28.99	0.32	9.47	0.07	83.33	1	1	2.00	0.34
Jan 20	Caulín	499	310	0.80	3.00	25.24	0.26	6.62	0.05	93.94	1	1	3.00	0.40
Jan 21	Chamiza-Sur	217	75	0.60	3.00	16.82	0.17	3.89	0.03	82.50	0	0	3.00	0.99
Jan 21	Quillaipe	0	5	-	-	-	-	-	-	78.33	0	0	-	-
Jan 21	Lenca	0	10	-	-	-	-	-	-	10.00	0	0	-	-
Jan 22	Chamiza-Sur	1320	180	0.90	3.00	29.99	0.18	3.44	0.04	82.50	0	0	3.00	0.80
Jan 23	Huapilacuy	0	25	-	-	-	-	-	-	55.00	0	0	-	-
Jan 23	Pullihue-Puente	0	15	-	-	-	-	-	-	90.00	1	1	-	-
Jan 24	Huelden	0	20	-	-	-	-	-	-	5.00	0	0	-	-
Jan 24	Linao	42	90	0.60	3.00	22.08	0.18	3.89	0.08	19.17	0	0	1.00	0.23
Jan 24	Ancud	27	10	0.70	3.50	22.84	0.33	7.45	0.06	10.00	0	0	1.00	0.30
Jan 26	Calén	0	25	-	-	-	-	-	-	26.25	0	0	-	-
Jan 26	San Juan	314	40	1.20	3.00	21.80	0.17	3.60	0.03	88.00	1	1	1.00	0.80
Jan 27	Nercón	331	185	1.00	3.00	18.95	0.18	3.66	0.04	89.29	0	0	3.00	0.71
Jan 27	Nercón-Puente	24	5	0.00	0.00	NA	NA	NA	NA	88.33	0	0	0.00	NA
Jan 27	Ten Ten	0	5	-	-	-	-	-	-	95.00	0	0	-	-
Jan 28	Pullao	558	245	1.10	3.00	22.75	0.30	6.98	0.06	96.25	0	0	1.00	0.24
Jan 28	Rilán	0	5	-	-	-	-	-	-	90.00	0	0	-	-
Jan 29	Curaco de Vélez	661	360	0.90	3.00	16.28	0.42	6.96	0.21	97.92	1	1	8.00	0.24
Jan 30	Chúllec	1055	360	0.80	3.00	20.29	0.27	6.97	0.07	90.00	6	5	12.00	0.35

TABLE DI (CONTINUED)

Date	Location	Flock size per km	Length of Survey (min)	Body Molt Score	Abdominal Profile Index	Probes per min	Success Rate	Swallows per min	Success Rate per min	% Mud and Algae	Number of Predators	Number of Predator Species	Number of Flushes	Alert per min
Jan 31	Aucar	9	85	0.80	3.00	21.43	0.31	6.23	0.06	15.00	1	1	0.00	0.90
Jan 31	Ancud	20	60	0.80	3.00	35.50	0.24	7.84	0.05	10.00	0	0	0.00	1.44
Feb 01	Quetalmahue-Puente	909	160	1.00	1.00	20.33	0.30	5.43	0.06	83.33	0	0	0.00	0.50
Feb 01	Piluco	118	90	1.00	3.00	23.11	0.20	4.68	0.04	25.00	0	0	2.00	1.10
Feb 02	Caulín	416	325	1.00	3.00	24.87	0.31	7.44	0.06	91.00	1	1	3.00	0.32
Feb 03	Linao	68	165	1.40	3.00	17.35	0.14	2.98	0.03	16.67	0	0	3.00	0.89
Feb 03	Caulín	222	20	0.00	0.00	NA	NA	NA	NA	93.94	0	0	2.00	NA
Feb 04	San Juan	83	180	0.80	3.00	24.62	0.09	2.15	0.03	88.00	0	0	1.00	0.36
Feb 04	Quetalco	43	70	0.90	3.00	27.43	0.18	4.95	0.04	71.67	0	0	1.00	0.59
Feb 05	Pullihue-Puente	1	35	0.00	3.00	18.92	0.37	6.97	0.07	90.00	0	0	0.00	0.80
Feb 05	Huapilacuy	0	45	-	-	-	-	-	-	55.00	0	0	-	-
Feb 05	Quetalmahue-Este	11	25	1.30	3.00	5.79	0.03	0.30	0.01	45.00	0	0	0.00	0.16
Feb 07	Chacao	55	5	1.50	3.00	29.13	0.38	11.16	0.07	13.33	0	0	0.00	0.64
Feb 07	Huelden	0	35	-	-	-	-	-	-	5.00	0	0	-	-
Feb 07	Manao	296	155	1.40	3.00	21.03	0.18	3.13	0.03	66.00	0	0	10.00	0.41
Feb 08	Ancud	4	30	1.10	3.00	22.84	0.33	7.45	0.06	10.00	0	0	2.00	0.30
Feb 08	Aucar	76	100	1.10	3.00	15.74	0.12	1.65	0.02	15.00	0	0	0.00	0.92
Feb 09	Calén	89	105	1.40	3.00	19.12	0.11	2.22	0.03	52.50	0	0	2.00	1.33
Feb 10	Pullao	310	210	2.00	3.00	17.45	0.19	3.35	0.05	95.00	0	0	6.00	0.50
Feb 10	Rilán	0	25	-	-	-	-	-	-	90.00	0	0	-	-
Feb 11	Nercón	409	175	1.70	3.00	32.44	0.18	4.54	0.02	89.29	0	0	4.00	0.25
Feb 11	Llicaldad-Sur	387	50	1.90	3.00	14.92	0.20	3.00	0.00	42.50	0	0	0.00	0.89
Feb 11	Nercón-Puente	24	5	1.80	3.00	NA	NA	NA	NA	88.33	0	0	0.00	NA
Feb 11	Ten Ten	0	5	-	-	-	-	-	-	95.00	0	0	-	-
Feb 12	Curaco de Vélez	7	5	0.00	0.00	NA	NA	NA	NA	97.92	0	0	0.00	NA
Feb 12	Chúllec	0	5	-	-	-	-	-	-	90.00	0	0	-	0.00
Feb 12	Quinchao	0	15	-	-	-	-	-	-	80.00	0	0	-	0.00
Feb 12	Achao	84	125	1.60	3.00	20.24	0.09	1.94	0.02	93.33	1	1	3.00	0.29
Feb 12	Chúllec	251	60	0.00	0.00	NA	NA	NA	NA	85.00	1	1	3.00	NA
Feb 13	Curaco de Vélez	72	140	1.60	3.00	25.49	0.17	4.28	0.03	100.00	1	1	1.00	0.05
Feb 13	Chúllec	0	10	-	-	-	-	-	-	90.00	1	1	-	-
Feb 13	Astillero	247	60	1.80	3.00	NA	NA	NA	NA	95.00	0	0	0.00	NA

TABLE DI (CONTINUED)

Date	Location	Flock size per km	Length of Survey (min)	Body Molt Score	Abdominal Profile Index	Probes per min	Success Rate	Swallows per min	Success Rate per min	% Mud and Algae	Number of Predators	Number of Predator Species	Number of Flushes	Alert per min
Feb 15	Contuy	119	105	1.90	3.00	20.61	0.29	5.64	0.09	91.25	0	0	3.00	0.27
Feb 15	Contuy-Oeste	368	10	0.00	0.00	NA	NA	NA	NA	60.00	0	0	0.00	NA
Feb 15	Compu	128	150	2.10	3.00	27.47	0.38	11.37	0.08	27.50	2	1	4.00	0.13
Feb 16	Yaldad	81	60	2.30	3.00	12.88	0.05	0.70	0.01	85.00	1	1	2.00	0.93
Feb 16	Quellón	148	25	0.00	0.00	NA	NA	NA	NA	90.00	0	0	0.00	NA
Feb 17	Nercón	1	5	0.00	0.00	NA	NA	NA	NA	89.29	0	0	0.00	NA
Feb 17	Nercón-Puente	625	100	1.60	3.00	25.03	0.13	3.34	0.03	88.33	0	0	1.00	0.53
Feb 18	Quetalmahue-Oeste	464	200	2.50	3.00	23.31	0.30	6.33	0.06	96.67	0	0	2.00	0.46
Feb 18	Quetalmahue-Puente	727	40	0.00	0.00	NA	NA	NA	NA	83.33	0	0	0.00	NA
Feb 19	Caulín	693	210	1.90	3.00	21.50	0.14	3.54	0.05	95.00	0	0	11.00	0.47
Feb 20	Manao	111	140	2.30	3.00	22.92	0.16	3.21	0.04	72.50	0	0	3.00	0.46
Feb 20	Linao	21	160	1.70	4.00	15.45	0.23	3.55	0.05	21.67	0	0	0.00	1.09
Feb 21	Teguel	284	135	2.30	3.00	15.38	0.19	3.30	0.04	78.00	5	4	7.00	0.28
Feb 22	Ten Ten	1	55	2.00	3.00	16.20	0.08	1.30	0.02	100.00	0	0	0.00	0.80
Feb 22	Putemún	0	10	-	-	-	-	-	-	55.00	0	0	-	-
Feb 22	Astillero	234	60	2.50	3.00	34.94	0.62	24.18	0.13	62.50	0	0	1.00	0.20
Feb 22	Llicaldad-Sur	0	85	-	-	-	-	-	-	30.00	0	0	-	-
Feb 22	Llicaldad	21	85	2.70	3.00	21.45	0.18	3.67	0.04	85.00	0	0	2.00	0.40
Feb 23	Pullao	12	10	0.00	0.00	NA	NA	NA	NA	72.50	0	0	0.00	NA
Feb 23	Ichuac	0	15	-	-	-	-	-	-	60.00	0	0	-	-
Feb 23	Aldachildo	36	60	2.30	3.00	NA	NA	NA	NA	2.50	0	0	1.00	NA
Feb 24	Achao	213	110	2.40	3.00	15.59	0.13	2.38	0.06	75.00	0	0	4.00	0.10
Feb 25	Chúllec	0	20	-	-	-	-	-	-	90.00	0	0	-	-
Feb 25	Curaco de Vélez	0	20	-	-	-	-	-	-	95.00	0	0	-	-
Feb 25	Astillero	51	15	2.30	3.00	20.32	0.31	6.37	0.06	90.00	0	0	1.00	0.80
Feb 25	Ten Ten	7	15	2.80	3.00	NA	NA	NA	NA	90.00	0	0	1.00	NA
Feb 26	Contuy	153	170	2.60	3.00	22.94	0.19	4.46	0.05	100.00	0	0	0.00	0.14
Feb 26	Contuy-Oeste	6	20	0.00	0.00	NA	NA	NA	NA	60.00	0	0	1.00	NA
Feb 27	San Juan	185	120	2.50	3.00	20.62	0.16	3.31	0.04	88.00	0	0	4.00	0.16
Feb 27	Teguel	523	90	2.70	3.00	17.20	0.19	3.35	0.05	67.50	1	1	5.00	0.34
Feb 29	Caulín	582	365	2.70	3.00	22.85	0.29	6.41	0.06	95.83	3	2	18.00	2.48
Mar 01	Quetalmahue-Oeste	29	5	0.00	0.00	NA	NA	NA	NA	96.67	0	0	0.00	NA

TABLE DI (CONTINUED)

Date	Location	Flock size per km	Length of Survey (min)	Body Molt Score	Abdominal Profile Index	Probes per min	Success Rate	Swallows per min	Success Rate per min	% Mud and Algae	Number of Predators	Number of Predator Species	Number of Flushes	Alert per min
Mar 01	Quetalmahue-Puente	727	280	2.80	3.00	27.31	0.37	8.37	0.34	83.33	3	1	11.00	0.46
Mar 02	Calén	0	10	-	-	-	-	-	-	0.00	0	0	-	-
Mar 02	San Juan	6	15	0.00	0.00	NA	NA	NA	NA	20.00	0	0	0.00	NA
Mar 02	Pullao	141	155	2.80	3.00	22.01	0.45	9.44	0.09	97.50	0	0	5.00	0.23
Mar 03	Compu	114	180	2.90	4.00	24.08	0.32	7.96	0.06	47.50	0	0	0.00	0.23
Mar 03	Contuy	0	5	-	-	-	-	-	-	98.75	0	0	-	-
Mar 03	Contuy-Oeste	126	105	2.60	4.00	22.67	0.28	6.37	0.07	60.00	0	0	2.00	0.11
Mar 03	Ten Ten	120	10	0.00	0.00	NA	NA	NA	NA	95.00	0	0	0.00	NA
Mar 04	Curaco de Vélez	160	120	2.90	3.00	21.67	0.30	6.48	0.09	98.75	0	0	6.00	0.24
Mar 04	Chúllec	151	7	0.00	0.00	NA	NA	NA	NA	90.00	0	0	1.00	NA
Mar 04	Achao	175	145	2.70	3.00	21.94	0.10	2.36	0.03	89.00	3	1	13.00	0.85
Mar 05	Aldachildo	32	85	3.00	4.00	16.82	0.12	1.64	0.02	10.00	0	0	0.00	2.23
Mar 05	Ichuac	17	50	2.30	3.00	18.84	0.27	4.77	0.11	90.00	0	0	1.00	0.61
Mar 06	Chamiza-Norte	104	100	3.30	4.00	32.77	0.23	7.42	0.05	100.00	0	0	2.00	0.60
Mar 06	Chamiza-Sur	231	85	3.00	4.00	22.84	0.13	3.00	0.03	92.50	0	0	3.00	0.21
Mar 07	Lenca	0	45	-	-	-	-	-	-	10.00	0	0	-	-
Mar 07	Quillaipe	76	85	2.50	3.00	19.87	0.12	2.61	0.06	78.33	0	0	6.00	1.18
Mar 08	Chamiza-Sur	198	125	3.60	4.00	26.67	0.15	3.80	0.03	72.50	0	0	0.00	0.04

Table DII. Survey data of non-breeding season human disturbances on Chiloé Island, Chile in 2016 for patch quality analysis of non-breeding habitat for Hudsonian Godwits (*Limosa haemastica*). A five meter buffer was used to indicate disturbances at the tideline, and a hundred meter buffer was used to indicate disturbances near foraging godwits.

Date	Location	Number of Humans	Number of Humans at Tideline	Number of Humans near Godwits	Number of Dogs	Number of Dogs at Tideline	Number of Dogs near Godwits	Number of Hoofed Animals	Number of Hoofed Animals at Tideline	Number of Hoofed Animals near Godwits	Number of Boats	Number of Boats at Tideline	Number of Boats near Godwits
Jan 02	Chacao	12.00	3.00	2.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 03	Aucar	2.00	0.33	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 03	Ancud	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 04	Caulín	4.13	1.25	0.33	0.50	0.25	0.14	0.50	0.00	0.00	0.00	0.00	0.00
Jan 05	Quetalmahue-Oeste	2.00	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 05	Quetalmahue-Puente	4.00	4.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 05	Quetalmahue-Este	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 05	Piluco	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 06	Quetalmahue-Puente	5.00	1.25	3.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 06	Quetalmahue-Oeste	10.00	10.00	0.00	0.00	0.00	0.00	2.00	2.00	0.00	0.00	0.00	0.00
Jan 06	Quetalmahue-Este	3.00	3.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 06	Piluco	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 07	Linao	6.10	4.60	5.80	0.20	0.20	0.20	0.00	0.00	0.00	0.50	0.30	0.30
Jan 08	Manao	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 08	Caulín	6.83	3.67	0.67	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 09	Aucar	0.40	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 09	Ten Ten	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 09	Putemún	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 09	Rilán	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 11	Putemún	30.67	16.67	2.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 11	Ten Ten	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 11	Nercón	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 11	Llicaldad	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 11	Nercón	7.00	3.00	1.00	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 11	Nercón-Puente	7.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 11	Nercón	10.00	4.50	3.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 11	Llicaldad	10.00	5.00	0.00	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 12	Pullao	0.38	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00
Jan 13	Ten Ten	6.00	2.00	1.50	3.50	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 13	Rilán	3.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 13	Putemún	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 14	Ten Ten	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 14	Curaco de Vélez	4.67	1.67	0.83	1.33	0.00	0.33	0.17	0.00	0.00	1.00	0.00	0.00

TABLE DII (CONTINUED)

Date	Location	Number of Humans	Number of Humans at Tideline	Number of Humans near Godwits	Number of Dogs	Number of Dogs at Tideline	Number of Dogs near Godwits	Number of Hoofed Animals	Number of Hoofed Animals at Tideline	Number of Hoofed Animals near Godwits	Number of Boats	Number of Boats at Tideline	Number of Boats near Godwits
Jan 15	Chúllec	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 15	Quinchao	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 15	Achao	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 15	Curaco de Vélez	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 16	Compu	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 16	Huildad	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 16	Quellón	2.00	0.00	0.00	1.50	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.50
Jan 17	Yaldad	10.00	0.00	3.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 18	Teguel	2.00	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 18	Quetalco	5.50	4.50	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.50	0.50	0.00
Jan 18	San Juan	4.00	2.00	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
Jan 19	Quetalmahue-Oeste	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 19	Quetalmahue-Puente	7.67	2.33	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 20	Caulín	7.83	2.67	1.17	0.33	0.00	0.33	0.50	0.50	0.00	0.67	0.17	0.17
Jan 21	Chamiza-Sur	30.50	11.00	5.50	1.50	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 21	Quillaipe	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 21	Lenca	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 22	Chamiza-Sur	10.33	10.00	6.00	4.50	4.00	4.50	1.33	2.00	0.00	0.00	0.00	0.00
Jan 23	Huapilacuy	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 23	Pullihue-Puente	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 24	Huelden	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 24	Linao	20.00	8.50	7.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00
Jan 24	Ancud	2.00	2.00	2.00	1.50	1.00	1.50	0.00	0.00	0.00	7.00	1.00	1.00
Jan 26	Calén	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 26	San Juan	7.00	1.67	0.33	2.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 27	Nercón	3.60	2.00	0.00	0.80	0.40	0.40	0.00	0.00	0.00	0.20	0.00	0.00
Jan 27	Nercón-Puente	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 27	Ten Ten	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jan 28	Pullao	2.60	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00
Jan 28	Rilán	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 29	Curaco de Vélez	3.86	0.00	0.00	0.86	0.43	0.43	0.00	0.00	0.00	0.00	0.00	0.00

TABLE DII (CONTINUED)

Date	Location	Number of Humans	Number of Humans at Tideline	Number of Humans near Godwits	Number of Dogs	Number of Dogs at Tideline	Number of Dogs near Godwits	Number of Hoofed Animals	Number of Hoofed Animals at Tideline	Number of Hoofed Animals near Godwits	Number of Boats	Number of Boats at Tideline	Number of Boats near Godwits
Jan 30	Chúllec	2.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 31	Aucar	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jan 31	Ancud	5.50	2.50	4.50	2.00	0.00	1.50	0.00	0.00	0.00	0.00	0.00	0.00
Feb 01	Quetalmahue-Puente	5.00	1.50	3.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 01	Piluco	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 02	Caulín	23.17	4.83	8.00	0.67	0.17	0.50	0.00	0.00	0.00	0.00	0.00	0.00
Feb 03	Linao	2.00	1.33	1.00	0.33	0.00	0.00	0.00	0.00	0.00	0.67	0.67	0.67
Feb 03	Caulín	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Feb 04	San Juan	8.33	2.33	1.67	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 04	Quetalco	2.50	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Feb 05	Pullihue-Puente	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 05	Huapilacuy	6.00	3.00	1.00	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 05	Quetalmahue-Harbor	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 07	Chacao	6.50	3.00	3.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 07	Huelden	10.00	8.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 07	Manao	13.67	10.67	2.00	1.00	0.67	0.00	0.00	0.00	0.00	1.00	0.33	0.33
Feb 08	Ancud	2.00	2.00	2.00	1.50	1.00	1.50	0.00	0.00	0.00	7.00	1.00	1.00
Feb 08	Aucar	4.50	4.50	0.00	1.50	1.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00
Feb 09	Calén	8.00	2.00	7.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 10	Pullao	4.67	1.33	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 10	Rilán	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 11	Nercón	16.00	7.67	9.00	3.00	2.67	1.67	0.00	0.00	0.00	0.00	0.00	0.00
Feb 11	Llicaldad-Sur	17.00	10.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 11	Nercón-Puente	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Feb 11	Ten Ten	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Feb 12	Curaco de Vélez	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 12	Chúllec	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Feb 12	Quinchao	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 12	Achao	3.60	0.25	0.75	1.80	0.25	0.25	0.00	0.00	0.00	0.60	0.00	0.25
Feb 12	Chúllec	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 13	Curaco de Vélez	5.00	0.67	1.33	0.00	0.00	0.00	3.33	3.33	3.33	0.00	0.00	0.00

TABLE DII (CONTINUED)

Date	Location	Number of Humans	Number of Humans at Tideline	Number of Humans near Godwits	Number of Dogs	Number of Dogs at Tideline	Number of Dogs near Godwits	Number of Hoofed Animals	Number of Hoofed Animals at Tideline	Number of Hoofed Animals near Godwits	Number of Boats	Number of Boats at Tideline	Number of Boats near Godwits
Feb 13	Chúllec	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 13	Astillero	3.50	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 15	Contuy	1.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00
Feb 15	Contuy-Oeste	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Feb 15	Compu	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 16	Yaldad	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 16	Quellón	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 17	Nercón	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Feb 17	Nercón-Puente	3.33	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 18	Quetalmahue-Oeste	6.20	3.40	3.20	0.40	0.20	0.20	0.40	0.40	0.40	0.00	0.00	0.00
Feb 18	Quetalmahue-Puente	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 19	Caulín	3.50	0.75	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 20	Manao	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 20	Linao	14.00	8.33	2.67	0.33	0.33	0.00	1.00	0.00	0.00	0.33	0.33	0.33
Feb 21	Teguel	0.67	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 22	Ten Ten	4.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 22	Putemún	0.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 22	Astillero	4.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 22	Llicaldad-Sur	9.00	7.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 22	Llicaldad	8.50	5.50	2.00	1.50	1.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00
Feb 23	Pullao	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 23	Ichuac	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 23	Aldachildo	8.00	8.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
Feb 24	Achao	10.50	3.00	2.00	2.00	1.80	1.80	0.00	0.00	0.00	0.67	0.00	0.67
Feb 25	Chúllec	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 25	Curaco de Vélez	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 25	Astillero	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 25	Ten Ten	7.00	7.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 26	Contuy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 26	Contuy-Oeste	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 27	San Juan	2.33	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TABLE DII (CONTINUED)

Date	Location	Number of Humans	Number of Humans at Tideline	Number of Humans near Godwits	Number of Dogs	Number of Dogs at Tideline	Number of Dogs near Godwits	Number of Hoofed Animals	Number of Hoofed Animals at Tideline	Number of Hoofed Animals near Godwits	Number of Boats	Number of Boats at Tideline	Number of Boats near Godwits
Feb 27	Teguel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Feb 29	Caulín	6.17	0.83	1.00	1.00	0.00	0.17	0.67	0.33	0.33	0.00	0.00	0.00
Mar 01	Quetalmahue-Oeste	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mar 01	Quetalmahue-Puente	3.20	2.20	2.80	0.40	0.40	0.40	0.00	0.00	0.00	0.00	0.00	0.00
Mar 02	Calén	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 02	San Juan	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 02	Pullao	1.33	0.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.33
Mar 03	Compu	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 03	Contuy	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mar 03	Contuy-Oeste	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 03	Ten Ten	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 04	Curaco de Vélez	6.00	2.67	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 04	Chúllec	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 04	Achao	19.67	6.33	14.67	2.00	1.00	1.33	0.00	0.00	0.00	0.00	0.00	0.00
Mar 05	Aldachildo	8.00	8.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
Mar 05	Ichuac	0.50	0.00	0.50	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00
Mar 06	Chamiza-Norte	1.00	1.00	1.00	2.00	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 06	Chamiza-Sur	15.00	8.00	9.00	3.00	3.00	3.00	2.00	2.00	2.00	0.00	0.00	0.00
Mar 07	Lenca	2.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mar 07	Quillaipe	5.00	3.50	5.00	1.50	1.50	1.50	1.00	1.00	1.00	0.00	0.00	0.00
Mar 08	Chamiza-Sur	11.50	3.50	2.50	4.50	1.00	2.50	4.50	2.00	2.00	0.00	0.00	0.00

Table DIII. Hudsonian Godwit (*Limosa haemastica*) flock counts, survey times, and low tide times at intertidal mudflats near Chiloé Island, Chile during patch quality surveys in 2016.

Date	Location	Time of Low Tide	Start Time of Survey	Maximum Flock Count
Jan 02 2016	Chacao	14:00	14:55	13
Jan 03 2016	Aucar	16:00	13:40	0
Jan 03 2016	Ancud	15:50	16:10	37
Jan 04 2016	Caulín	15:00	12:35	1,500
Jan 05 2016	Quetalmahue-Oeste	16:30	13:50	0
Jan 05 2016	Quetalmahue-Puente	16:30	14:55	1,000
Jan 05 2016	Quetalmahue-Este	16:30	16:10	72
Jan 05 2016	Piluco	16:30	16:30	250
Jan 06 2016	Quetalmahue-Puente	17:30	15:30	500
Jan 06 2016	Quetalmahue-Oeste	17:30	17:55	100
Jan 06 2016	Quetalmahue-Este	17:30	19:18	39
Jan 06 2016	Piluco	17:30	19:40	25
Jan 07 2016	Linao	18:00	14:25	475
Jan 08 2016	Manao	07:00	07:00	42
Jan 08 2016	Caulín	19:00	16:00	1,500
Jan 09 2016	Aucar	08:00	08:15	40
Jan 09 2016	Ten Ten	08:00	12:15	73
Jan 09 2016	Putemún	20:00	17:20	0
Jan 09 2016	Rilán	20:00	18:00	0
Jan 11 2016	Putemún	09:35	09:45	0
Jan 11 2016	Ten Ten	09:35	11:20	0
Jan 11 2016	Nercón	09:35	11:50	616
Jan 11 2016	Llicaldad	21:30	18:42	5
Jan 11 2016	Nercón	21:30	18:54	0
Jan 11 2016	Nercón-Puente	21:30	19:15	514
Jan 11 2016	Nercón	21:30	20:00	302
Jan 11 2016	Llicaldad	21:30	20:50	71
Jan 12 2016	Pullao	10:15	8:30	2,000
Jan 13 2016	Ten Ten	10:50	9:30	10
Jan 13 2016	Rilán	10:50	10:55	0
Jan 13 2016	Putemún	10:50	12:50	0
Jan 14 2016	Ten Ten	11:35	07:45	178
Jan 14 2016	Curaco de Vélez	11:35	09:00	4,450
Jan 15 2016	Chúllec	12:23	09:45	221
Jan 15 2016	Quinchao	12:23	12:15	0
Jan 15 2016	Achao	12:23	13:00	0
Jan 15 2016	Curaco de Vélez	12:23	13:35	0
Jan 16 2016	Compu	13:00	10:25	0
Jan 16 2016	Huildad	13:00	11:50	2,800
Jan 16 2016	Quellón	13:30	14:05	660
Jan 17 2016	Yaldad	14:45	11:50	670
Jan 18 2016	Teguel	15:45	13:45	7
Jan 18 2016	Quetalco	15:45	14:55	132
Jan 18 2016	San Juan	15:45	16:40	1,550
Jan 19 2016	Quetalmahue-Oeste	16:30	13:50	0
Jan 19 2016	Quetalmahue-Puente	15:20	14:05	800
Jan 20 2016	Caulín	16:20	13:40	1,800
Jan 21 2016	Chamiza-Sur	19:00	18:00	650
Jan 21 2016	Quillaipe	19:00	16:32	0
Jan 21 2016	Lenca	19:00	16:55	0
Jan 22 2016	Chamiza-Sur	19:45	17:00	4,000
Jan 23 2016	Huapilacuy	19:30	17:20	0
Jan 23 2016	Pullihue-Puente	19:30	18:05	0
Jan 24 2016	Huelden	08:30	09:15	0

TABLE DIII (CONTINUED)

Date	Location	Time of Low Tide	Start Time of Survey	Maximum Flock Count
Jan 24 2016	Linao	08:30	10:15	245
Jan 24 2016	Ancud	20:30	18:28	45
Jan 26 2016	Calén	10:15	10:45	0
Jan 26 2016	San Juan	10:15	12:00	850
Jan 27 2016	Nercón	10:45	09:05	510
Jan 27 2016	Nercón-Puente	10:45	12:15	20
Jan 27 2016	Ten Ten	10:45	12:35	0
Jan 28 2016	Pullao	11:15	08:55	2,250
Jan 28 2016	Rilán	11:15	13:25	0
Jan 29 2016	Curaco de Vélez	11:45	09:20	2,050
Jan 30 2016	Chúllec	12:10	09:20	2,400
Jan 31 2016	Aucar	13:15	12:35	21
Jan 31 2016	Ancud	12:15	15:05	49
Feb 01 2016	Quetalmahue-Puente	14:00	11:30	1,500
Feb 01 2016	Piluco	14:00	14:35	175
Feb 02 2016	Caulín	15:00	12:05	1,600
Feb 03 2016	Linao	17:20	14:35	480
Feb 03 2016	Caulín	17:20	18:00	800
Feb 04 2016	San Juan	17:50	14:50	225
Feb 04 2016	Quetalco	17:50	18:20	62
Feb 05 2016	Pullihue-Puente	18:00	15:40	1
Feb 05 2016	Huapilacuy	18:00	16:30	0
Feb 05 2016	Quetalmahue-Harbor	18:00	17:55	12
Feb 07 2016	Chacao	08:45	09:55	103
Feb 07 2016	Huelden	20:30	17:05	0
Feb 07 2016	Manao	20:30	18:05	800
Feb 08 2016	Ancud	09:00	08:35	7
Feb 08 2016	Aucar	09:00	10:05	177
Feb 09 2016	Calén	21:30	18:50	266
Feb 10 2016	Pullao	10:00	08:00	1,250
Feb 10 2016	Rilán	10:00	11:45	0
Feb 11 2016	Nercón	10:40	09:10	630
Feb 11 2016	Llicaldad-Sur	10:40	12:15	151
Feb 11 2016	Nercón-Puente	10:40	13:10	20
Feb 11 2016	Ten Ten	10:40	13:30	0
Feb 12 2016	Curaco de Vélez	11:30	08:57	22
Feb 12 2016	Chúllec	11:30	09:15	0
Feb 12 2016	Quinchao	11:30	09:35	0
Feb 12 2016	Achao	11:30	10:10	230
Feb 12 2016	Chúllec	11:30	12:40	500
Feb 13 2016	Curaco de Vélez	12:00	09:40	224
Feb 13 2016	Chúllec	12:00	12:20	0
Feb 13 2016	Astillero	12:00	13:00	292
Feb 15 2016	Contuy	14:15	11:25	850
Feb 15 2016	Contuy-Oeste	14:15	13:47	1,600
Feb 15 2016	Compu	14:50	14:30	505
Feb 16 2016	Yaldad	15:40	12:20	320
Feb 16 2016	Quellón	15:40	13:50	400
Feb 17 2016	Nercón	17:00	16:00	1
Feb 17 2016	Nercón-Puente	17:00	16:00	520
Feb 18 2016	Quetalmahue-Oeste	17:15	15:40	510
Feb 18 2016	Quetalmahue-Puente	17:15	19:10	1,200

TABLE DIII (CONTINUED)

Date	Location	Time of Low Tide	Start Time of Survey	Maximum Flock Count
Feb 19 2016	Caulín	19:30	16:20	2,500
Feb 20 2016	Manao	08:00	08:05	300
Feb 20 2016	Linao	20:00	17:00	122
Feb 21 2016	Teguel	20:20	17:20	435
Feb 22 2016	Ten Ten	08:45	08:40	2
Feb 22 2016	Putemún	08:40	10:00	0
Feb 22 2016	Astillero	08:40	10:40	276
Feb 22 2016	Llicaldad-Sur	20:50	18:40	0
Feb 22 2016	Llicaldad	20:50	18:40	8
Feb 23 2016	Pullao	09:15	09:05	60
Feb 23 2016	Ichuac	09:15	10:30	0
Feb 23 2016	Aldachildo	09:15	11:10	36
Feb 24 2016	Achao	09:45	10:00	425
Feb 25 2016	Chúllec	10:10	09:40	0
Feb 25 2016	Curaco de Vélez	10:10	10:10	0
Feb 25 2016	Astillero	10:10	11:15	60
Feb 25 2016	Ten Ten	10:10	12:00	13
Feb 26 2016	Contuy	10:50	09:45	1,100
Feb 26 2016	Contuy-Oeste	10:50	12:50	25
Feb 27 2016	San Juan	10:55	09:50	500
Feb 27 2016	Teguel	10:55	12:25	800
Feb 29 2016	Caulín	11:45	08:45	2,100
Mar 01 2016	Quetalmahue-Oeste	12:30	09:45	60
Mar 01 2016	Quetalmahue-Puente	12:30	10:00	1,200
Mar 02 2016	Calén	14:00	11:30	0
Mar 02 2016	San Juan	14:00	12:30	16
Mar 02 2016	Pullao	14:00	13:25	850
Mar 03 2016	Compu	16:10	13:00	450
Mar 03 2016	Contuy	16:10	16:30	0
Mar 03 2016	Contuy-Oeste	16:10	16:45	550
Mar 03 2016	Ten Ten	16:10	19:55	240
Mar 04 2016	Curaco de Vélez	17:20	14:20	497
Mar 04 2016	Chúllec	17:20	16:28	300
Mar 04 2016	Achao	17:20	16:55	400
Mar 05 2016	Aldachildo	18:10	15:35	32
Mar 05 2016	Ichuac	18:10	17:20	55
Mar 06 2016	Chamiza-Norte	19:00	15:50	600
Mar 06 2016	Chamiza-Sur	19:00	17:55	700
Mar 07 2016	Lenca	19:45	16:45	0
Mar 07 2016	Quillaipe	19:45	17:55	435
Mar 08 2016	Chamiza-Sur	08:20	08:55	600

APPENDIX E

Table EI. Beta estimates and 95% confidence intervals (CI) for generalized linear regressions against Julian date with a random effect of survey location.

	Beta	95% CI
Body Molt Score	0.05	(0.04, 0.05)
Abdominal Profile Index	0.01	(0.008, 0.01)
Probes per min	0.04	(-0.009, 0.08)
Swallows per min	0.02	(-0.002, 0.05)
Success Rate	0.001	(0.005, 0.002)
Success Rate per min	0.001	(0.00, 0.001)

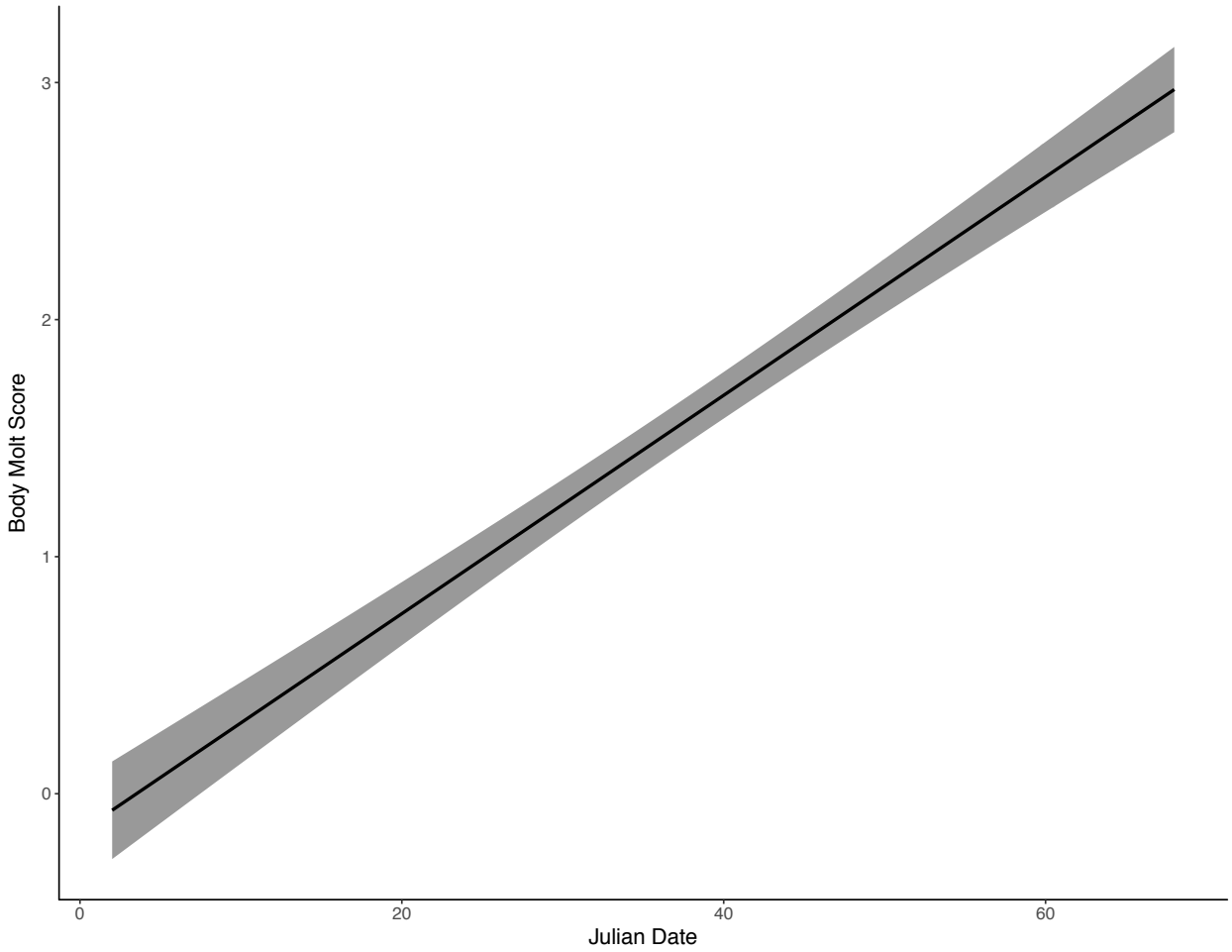


Figure E1. Hudsonian Godwit (*Limosa haemastica*) body molt scores increased during the late non-breeding season on Chiloé Island, Chile from January to March 2016. Ninety-five percent confidence intervals shown (gray area).

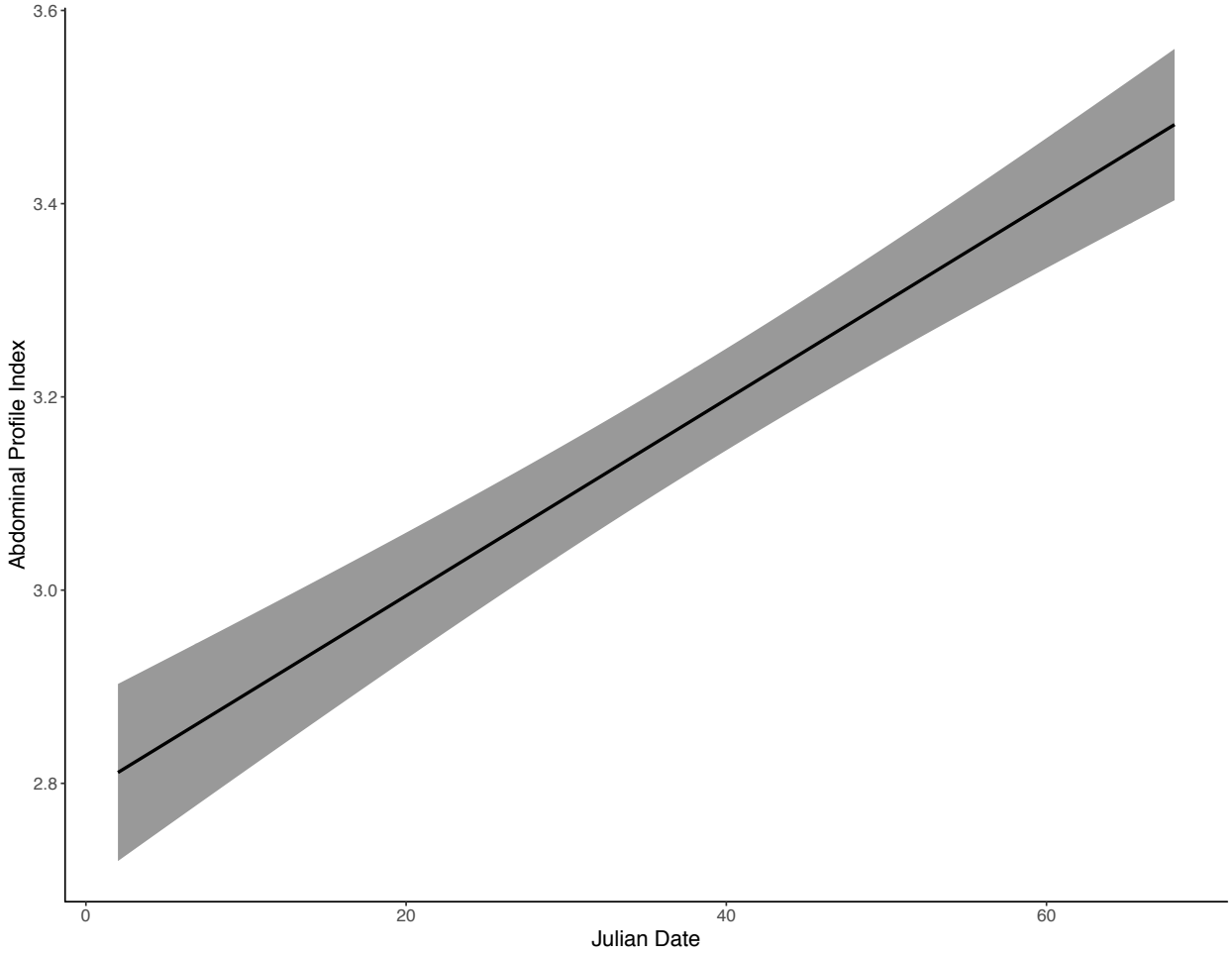


Figure E2. Hudsonian Godwit (*Limosa haemastica*) abdominal profile index increased during the late non-breeding season on Chiloé Island, Chile from January to March 2016. Ninety-five percent confidence intervals shown (gray area).

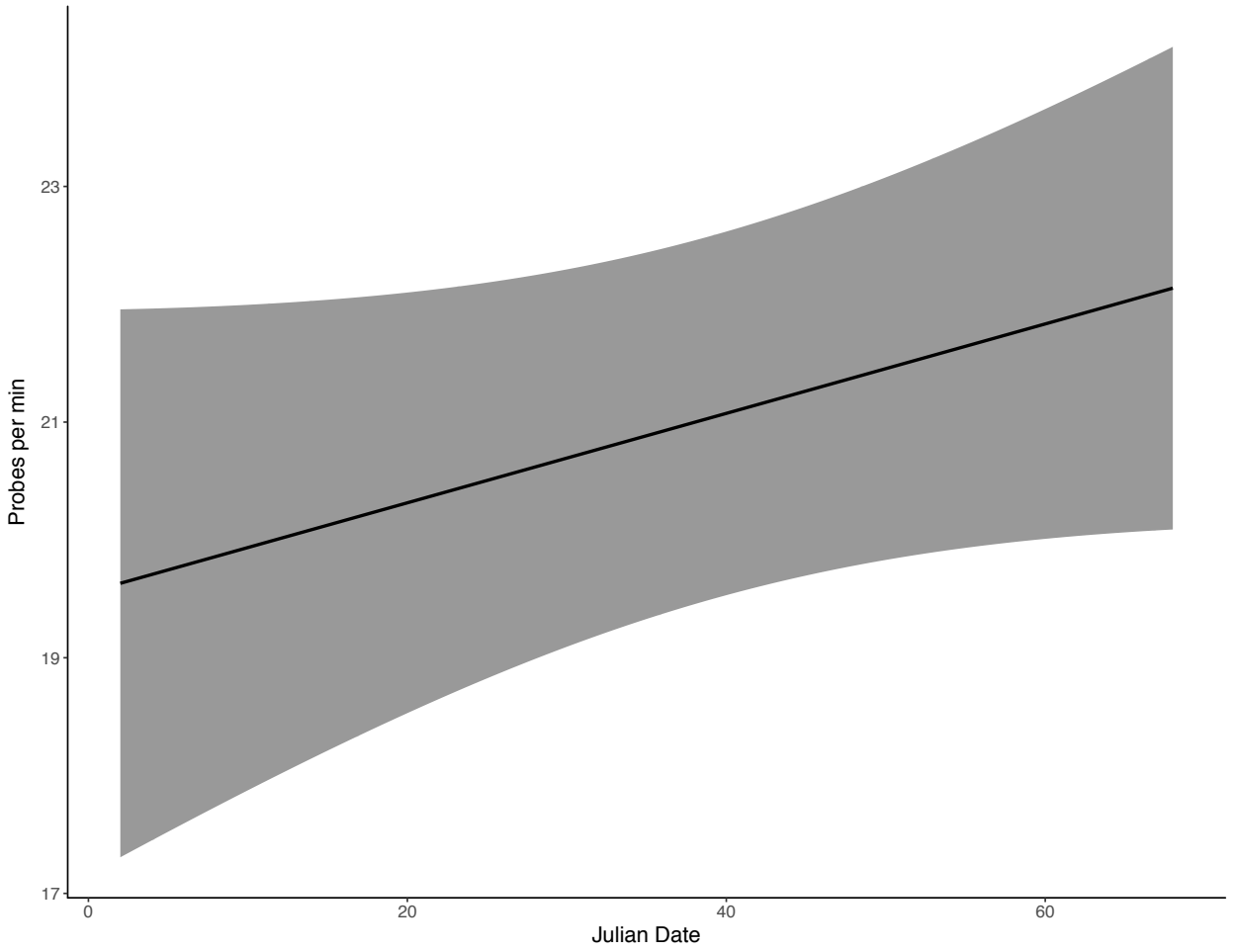


Figure E3. Hudsonian Godwit (*Limosa haemastica*) probes per minute increased during the late non-breeding season on Chiloé Island, Chile from January to March 2016. Ninety-five percent confidence intervals shown (gray area).

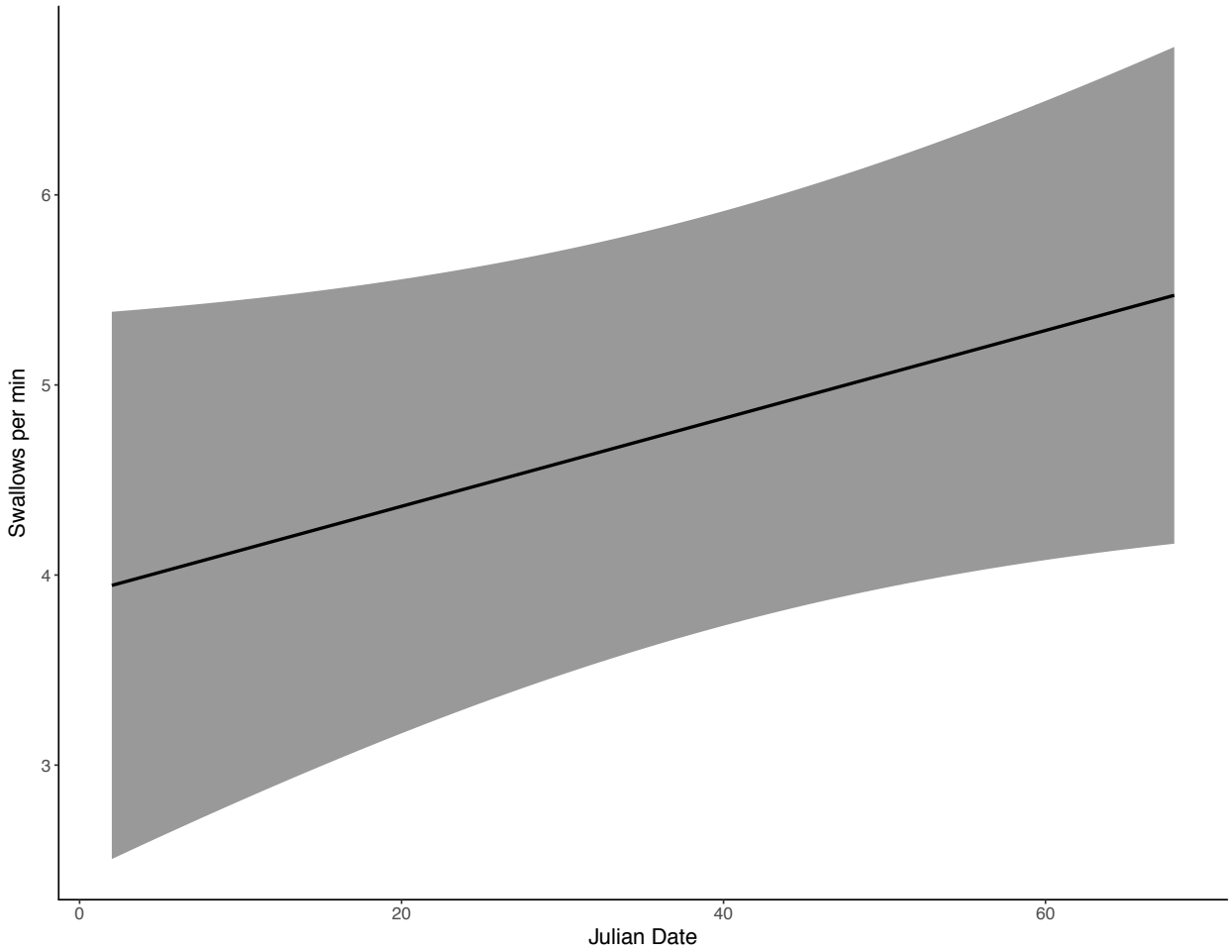


Figure E4. Hudsonian Godwit (*Limosa haemastica*) swallows per min increased during the late non-breeding season on Chiloé Island, Chile from January to March 2016. Ninety-five percent confidence intervals shown (gray area).

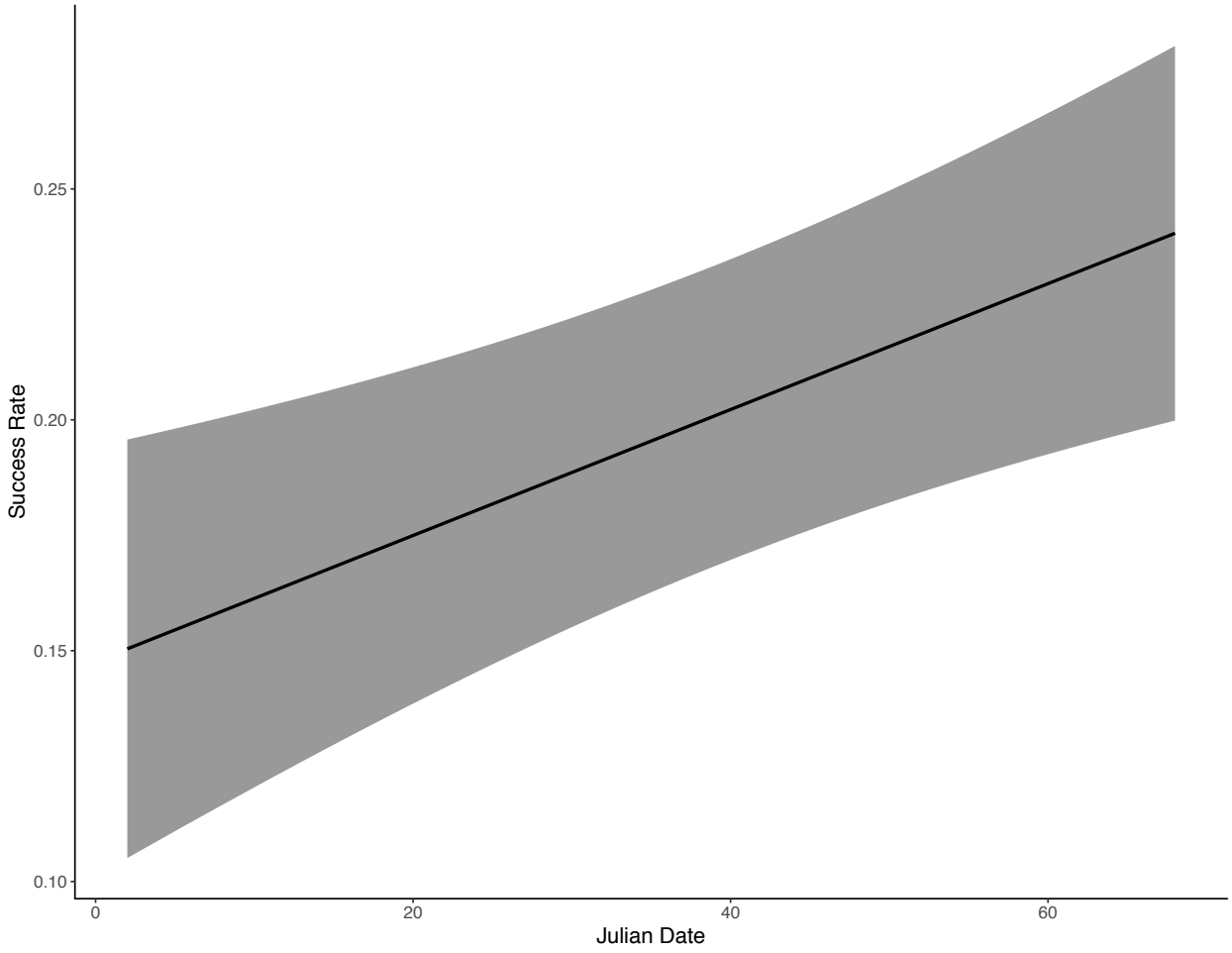


Figure E5. Hudsonian Godwit (*Limosa haemastica*) success rate increased during the late non-breeding season on Chiloé Island, Chile from January to March 2016. Ninety-five percent confidence intervals shown (gray area).

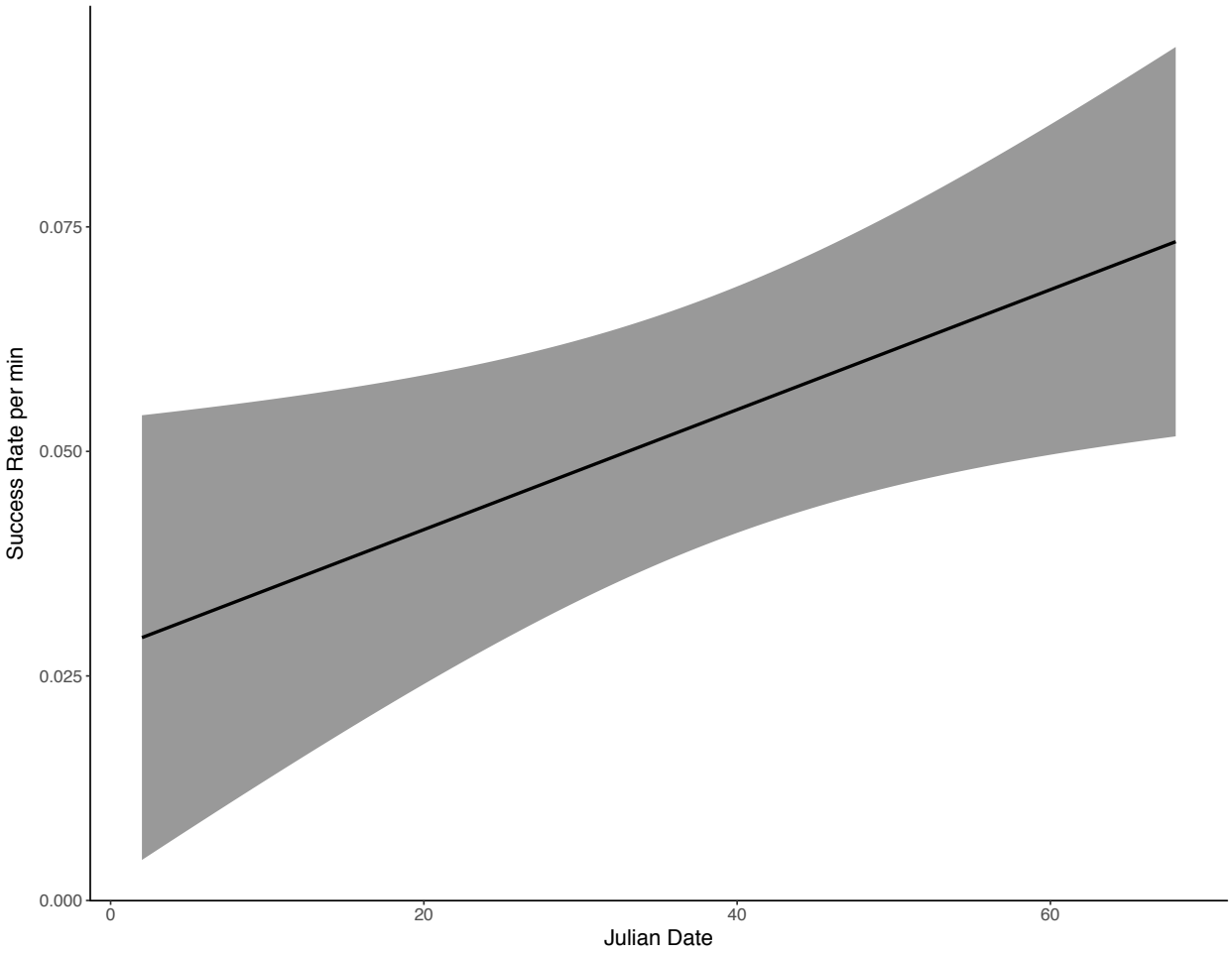


Figure E6. Hudsonian Godwit (*Limosa haemastica*) success rate per min increased during the late non-breeding season on Chiloé Island, Chile from January to March 2016. Ninety-five percent confidence intervals shown (gray area).

CHAPTER FIVE

SEASONAL SURVIVAL AND REVERSIBLE STATE EFFECTS IN A LONG-DISTANCE MIGRATORY SHOREBIRD

Abstract:

Events during any one part of the annual cycle can impact an individual's condition and survival within a given season, as well as its performance and fitness in subsequent seasons. These reversible state effects can occur during any stage of the annual cycle and ultimately affect population dynamics. Gathering such information can be, in turn, critical for developing targeted conservation objectives for at-risk and declining species. To identify possible cross-seasonal interactions in a declining long-distance migratory shorebird, we estimated period-specific survival probabilities across the annual cycle using two distinct marked populations of Hudsonian Godwits (*Limosa haemastica*). We then examined the extent to which body condition, foraging success, and habitat quality during the non-breeding season impacted return rates and reproductive performance during the following breeding season of 25 marked individuals monitored throughout their annual cycle. Survival rates were high throughout the annual cycle, with daily survival reaching the lowest levels during migration and highest during the stationary non-breeding season; nonetheless, the breeding season and southbound migration accounted for the largest proportion of mortality events. Our results provide evidence of reversible state effects, such that overwintering godwits that used the highest-quality habitats and were in the best body condition prior to spring migration performed best on the breeding grounds, exhibiting higher nest and chick survival than their poorer-condition counterparts. This finding was corroborated by an analysis of feather growth bars collected repeatedly from individuals over three years, which indicated that nutritional status on the non-breeding grounds was positively related to chick survival. Therefore, reversible state effects were acting across non-breeding to breeding seasons and influenced variation in seasonal survival rates of Hudsonian Godwits. Our understanding of cross-seasonal interactions benefits from linking

observations of individual performance with demography to identify conservation actions that connect individual behaviors to survival.

Keywords: cross-seasonal interactions, reproductive performance, body condition, foraging success, non-breeding season, ptilochronology, habitat quality

Introduction:

Migratory species face a variety of risks as they use widely dispersed sites throughout their annual cycle (Newton 2008). Determining the places and periods associated with the greatest mortality risk is essential for understanding population dynamics. By quantifying survival during distinct periods of the annual cycle, we can begin to assess actionable conservation goals by identifying population bottlenecks. Most research has thus far focused on documenting whether local populations experience limiting factors during the breeding season and to a lesser degree during the non-breeding season or migration (Pasinelli et al. 2011, Marra et al. 2015, Studds et al. 2017). Theoretical and empirical studies have demonstrated that the breeding abundance of migratory birds can be limited by breeding, stopover, or non-breeding habitat (Sherry and Holmes 1995, Sutherland 1996, Piersma et al. 2016). For instance, reliance on the Yellow Sea is the best predictor of declines for 10 species of shorebirds using the East Asian Australasian Flyway (Studds et al. 2017). Further, processes operating across the annual cycle can interact in complex ways at both the individual and population levels (Harrison et al. 2011). To effectively conserve migratory species, we must therefore work to understand the factors that limit survival and population growth and how these may be impacted by events occurring during different parts of the annual cycle.

Carry-over effects, which occur when events affecting an individual in one season alter the outcome of a subsequent season (although the concept can be broadened to other life stages and time-scales), have been demonstrated in many taxa including birds, mammals, fish, and invertebrates (Harrison et al. 2011, O'Connor et al. 2014, Senner et al. 2015). Although carry-over effects are generally considered to be non-lethal (Harrison et al. 2011, O'Connor et al. 2014), they can indirectly increase the risk of mortality resulting in lethal consequences (Norris

2005). Fitness consequences may not be readily apparent across short time scales and carry-over effects can even affect senescence or provoke maternal effects on offspring. Although some carry-over effects are irreversible (e.g., maternal effects), those experienced during adulthood may be reversible (e.g., 'reversible state effects'; Senner et al. 2015). Reversible state effects can carry-over to affect individual fitness during subsequent life-history stages but can be at least partially compensated for over time and need not repeatedly influence an individual's fitness ('compensation hypothesis'; Conklin et al. 2013, Senner et al. 2014, Clausen et al. 2015). If individuals cannot compensate, however, they may experience reduced breeding performance. Assessing the magnitude and consequences of seasonal interactions is thus critical for determining the factors influencing individual fitness and population dynamics (Norris and Marra 2007, Harrison et al. 2011).

For long-distance migrants, non-breeding season habitat quality, foraging success, and body condition are among those factors that can impact an individual's future breeding performance. The importance of these factors derives from the fact that successful migration to breeding areas in these species hinges on (i) the accumulation of sufficient energy stores to cover the costs of flight and (ii) appropriate departure and arrival timing that optimize the chances of reproduction. The quality of winter habitat can influence a bird's physiological stress levels (Marra and Holberton 1998), physical condition (Marra et al. 1998, Strong and Sherry 2001, Studds and Marra 2005), and departure timing for spring migration (Marra et al. 1998, Studds and Marra 2011), with cascading effects on the timing of arrival at breeding grounds and reproductive success (Marra et al. 1998, Norris et al. 2004). For example, Cassin's Auklets (*Ptychoramphus aleuticus*) that have a higher proportion of energetically superior copepods (*Neocalanus* spp.) in their pre-breeding diets breed earlier and lay larger eggs than individuals

with high proportions of energetically poor juvenile rockfish (*Sebastes* spp.; Sorensen et al. 2009). Reversible state effects can thus occur during different stages of the annual cycle and affect an individual's performance, and ultimately fitness, through a variety of mechanisms.

Identifying the seasons, and thus regions, when mortality is comparably high or low is vital to understand population dynamics. Demographic rates are affected by intrinsic (e.g., age, sex, experience) and extrinsic (e.g., habitat quality, food availability, climate) factors, which can directly influence demographic parameters through mortality or indirectly through reversible state effects (Szostek and Becker 2015). Few previous studies, however, have been able to directly connect events occurring across seasons with both variation in individual performance and changes in population-level survival rates. For instance, severe weather on the non-breeding grounds reduced adult survival during both the winter and the following breeding season in Eurasian Oystercatchers (*Haematopus ostralegus*; Duriez et al. 2012). Yet we remain challenged to understand how selective pressures are acting on a population both within and across seasons. Connecting reversible state effects to demographic survival studies is a necessary step to identify when bottlenecks occur during the annual cycle, as well as their underlying causes, helping to inform conservation actions.

To further explore the potential connections between reversible state effects and variation in survival rates across the annual cycle, we studied marked populations of Hudsonian Godwits (*Limosa haemastica*; hereafter 'godwits') during both the non-breeding and breeding seasons. This enables us to identify whether reversible state effects were acting across these time periods and, if so, determine how they influenced seasonal survival rates. Godwits breed in three geographically distinct populations across the Nearctic that each show high connectivity to disjunct non-breeding grounds in the Southern Cone of South America. Further, each of these

populations is thought to be declining (Andres et al. 2012, Smith et al. unpubl. data) largely for unknown reasons. We thus aimed to identify potential bottlenecks in the annual cycle of the population of godwits breeding in south-central Alaska and spending the non-breeding season on or near Chiloé Island, Chile. To do this, we first estimated seasonal survival probabilities across the annual cycle using two distinct, marked populations. Second, we examined how non-breeding body condition, habitat quality, and foraging success influenced breeding performance using a marked population that can be followed throughout their annual cycle. Third, we used ptilochronology to examine potential reversible state effects of an individual's non-breeding season nutritional status on their future breeding performance. Our study used a unique approach to evaluate reversible state effects by corroborating direct observations of the same individuals during two stages of the annual cycle with indirect measures via ptilochronology. We then linked our measures of individual performance with the first seasonal survival analysis for this species to integrate direct and indirect effects of seasonal interactions on population dynamics. Our study improves our understanding of the full annual cycle of long-distance migrants, aiding our ability to conserve these rapidly declining species.

Methods:

Study Species:

We studied a linked, marked population of Hudsonian Godwits that breed in south-central Alaska (Beluga River) and spend the non-breeding season on Chiloé Island in southern Chile (Senner et al. 2014). With annual declines of 3.45% over the last 30 years, the Hudsonian Godwit is among the fastest declining shorebird species breeding in North America (Smith et al. unpubl. data).

The non-breeding season is a critical period for godwits and one likely to be associated with reversible state effects. During the 192 days (~27 weeks) godwits spend on the non-breeding grounds (Espinosa et al. 2005, Senner et al. 2014), individuals must recover from their southward migration, undergo two separate molts, and prepare for their northward migration and breeding season (Conklin and Battley 2012). Godwits are typically found foraging in large flocks on tidal mudflats along sheltered coastlines (García-Walther et al. 2017). The connectivity and movements of individual godwits in the Chiloé region are poorly understood, but individuals are known to move among bays in response to disturbances, predators, tides, and weather (Andres et al. 2009). Indeed, color-marked individuals have been resighted at bays separated by as much as 40 km (NR Senner and RJ Swift unpubl. data).

Godwits exhibit a cyclical, long-leap migration strategy. Upon leaving the non-breeding grounds, godwits undertake a 10,000 km non-stop flight to the Great Plains of the United States in as little as 6 – 7 days before completing a second non-stop flight to reach their Alaskan breeding grounds. Individuals are highly consistent in the timing of northbound migration across years, regardless of arrival date to the non-breeding grounds (Senner et al. 2014). During southbound migration, individuals stage in the pothole lakes of central Saskatchewan for approximately one month before undertaking several non-stop flights of 3-5 days during southbound migration. Most individuals fly over the Atlantic Ocean to stopover sites in the Amazon River Basin in Colómbia and Brazil and then on to the Buenos Aires Province, Argentina before arriving on the non-breeding grounds. Southward migration is more protracted than northward migration and typically lasts 11 – 12 weeks (Senner et al. 2014).

The breeding season clearly impacts fitness and population dynamics for godwits. Godwits arrive to the breeding grounds synchronously and initiate breeding within a week of

arrival. Individuals show high fidelity to mates and territories and exhibit biparental care (Walker et al. 2011). Nest survival is high, with >80% of nests successfully hatching, but brood survival can be quite variable (Senner et al. 2017, Swift et al. 2018). Renesting propensity is high (~75%) if nests fail early in incubation (Walker et al. 2011). Godwits nest both within and outside of a protective nesting association with Mew Gulls (*Larus canus*) in non-habitat based clusters (Swift et al. 2017, Swift et al. 2018). The breeding season is relatively short, from May to early July, and individuals typically spend 10 – 11 weeks on the breeding grounds (Senner et al. 2014). Adults leave the breeding grounds immediately following the completion of the breeding season.

Seasonal Survival:

Field methods:

We studied godwits during two time periods and at two locations during the annual cycle: (i) from 2007 – 2012 during the non-breeding season on Chiloé Island, Chile; and (ii) from 2009 – 2012 and 2014 – 2017 during the breeding season at Beluga River, Alaska (Figure 1). We visited the Chilean site (~42°30'S, 73°45'W) for a single two-week period annually in December or January. We visited one tidal mudflat, Pullao, daily to resight marked individuals. In addition, we surveyed several nearby tidal mudflats in the Castro region on Chiloé Island as time allowed and when flocks were present (e.g., Putemún, Rilán, Curaco de Vélez, Chúllec, Teguel, and Ten-Ten). During the breeding season, we monitored godwits within an ~8 km^2 area at Beluga River, Alaska (61.21°N, 151.03°W) between 1 May and mid-July. We resighted godwits at their nest, on nearby tidal mudflats, or during the brood rearing period within the bogs. Physical recaptures of incubating individuals were also added to the resighting data. In 2017, we only conducted a shortened field season for resightings from 9 – 19 May.

Survival estimates were based on resightings of marked individuals. Returning birds were rarely missed in our surveys on the breeding grounds, but movements of individuals among tidal mudflats on the non-breeding grounds reduced resighting probabilities. Individually marked godwits breeding at our Alaska site are regularly resighted on Chiloé Island, but individuals marked at our Chile site are only rarely seen on the breeding grounds. Each year from 2007 – 2011, we made an effort to capture additional godwits in Chile using cannon nests to add to the marked population. Unmarked individuals on the breeding grounds were captured with a mist net while incubating their nests (see Chapter 3 for more information). In total, our Chilean dataset consisted of 773 marked birds, and the Alaskan dataset 118 marked adults. All individuals were marked with a uniquely coded alpha-numeric flag and metal band from the US Geological Survey (Alaska) or Chilean Bird Ringing Office (Chile).

Data analysis:

Survival (φ) and recapture (p) probabilities were modeled annually as well as within each stationary season. Sampling in Chile occurred during a two-week period in either December or January. To account for movements of individuals among mudflats and the imperfect detection of individuals within large flocks, we aggregated observations of individuals into three-to-four day windows across the study period. We then modeled encounters among these windows and with an additional resighting period in the following non-breeding season for the 2009 – 2010 and 2010 – 2011 non-breeding seasons. In Alaska, godwits were systematically resighted every 1 – 7 days from early-May to mid-July. We broke the breeding season down into one-week intervals from 1 May until the earliest recorded egg hatch date in our study (4 June; five weeks).

We combined all resightings post-incubation into one additional sampling period to account for individuals departing the breeding grounds immediately following nest or brood failure.

Sets of candidate models were chosen prior to data analysis based on our knowledge of godwit biology and model goodness-of-fit (Burnham and Anderson 2002). For annual survival models, the base model for each model set included all time and group variables hypothesized to affect φ and p. Fit of global models was verified in program U-CARE (Choquet et al. 2009), as well as program RELEASE (Burnham et al. 1987) implemented in program RMark (Laake 2013). If models failed to meet goodness-of-fit criteria, we calculated the median c-hat value and adjusted our results table accordingly using $QAIC_C$ values. Time and group variables used in candidate models are described below. Model notation follows Lebreton et al. (1992).

In annual analyses, φ and p were modeled as either constant over time, as a function of year or sex, or as an interactive effect of year and sex. In seasonal analyses, φ and p were modeled as either constant over time, or as a function of time (e.g., different φ time for each encounter period) or sex. We did not model the interactive effect between sex and time within a season due to poor model fit.

To determine each individual's sex on the non-breeding grounds, we used a linear discriminant function analysis on the length of the tarsus (mm) and culmen (mm) of 228 captures of known-sex individuals from the breeding grounds. We conservatively placed 137 individuals captured in Chile (17.6%) into an 'unknown sex' category based on their measurements.

Model selection methods based on Akaike's information criterion corrected for small sample sizes (AIC_C; Burnham and Anderson 2002) were used to (i) provide the best estimates of annual and within season φ for godwits; and (ii) assess the statistical evidence for time- and sex-related differences in φ. Models in each candidate set were ranked by $dAIC_C$ (or $QAIC_C$)

differences (Burnham and Anderson 2002). Program MARK's model averaging procedure was used to compute the average estimates for φ from all models selected. Model averaging is based on model weights for each model and thus includes model selection uncertainty in the estimate of each parameter and its associated variance (Burnham and Anderson 2002).

Annual survival probability is the product of survival probabilities during the stationary and migratory periods of the annual cycle, i.e., $\varphi_{annual} = \varphi_{non\text{-}breeding} * \varphi_{breeding} * \varphi_{migration}$. We considered φ_{annual} to be survival from January to January as measured in Chile or from May to May as measured in Alaska, $\varphi_{breeding}$ from May to July in Alaska (11 weeks), and $\varphi_{non\text{-}breeding}$ from October to March in Chile (27 weeks). This equation allowed us to use within-season estimates of φ from Alaska and Chile to estimate survival during the migratory periods as $\varphi_{migration}$: (φ_{annual} / $\varphi_{(non\text{-}breeding * breeding)}$). Because our annual survival estimates differed between our breeding and non-breeding season analyses (see Results), we present a range for our estimate of $\varphi_{migration}$. Because our data were not amenable to calculating robust, year-specific estimates of $\varphi_{migration}$, we did not compute survival probabilities separately for northbound and southbound migration. Survival probability during the migratory period was broken down to weekly estimates and then calculated for the length of the northbound and southbound migration (3 and 11 weeks, respectively) to enable a direct comparison of survivorship among periods.

Reversible state effects:

Observational study:

Field Methods – non-breeding season:

We attempted to survey all known and accessible tidal mudflats based on published distributions, eBird records, and prior knowledge of the occurrence of flocks of foraging godwits

for marked individuals from our breeding population (2015: n = 39 surveys at 21 tidal mudflats; 2016: n = 147 surveys at 42 tidal mudflats). Surveys occurred from 3 – 16 January 2015 and 1 January – 8 March 2016. During a survey, each individual present at a site was checked for leg flags from our marked breeding population and, if marked, identified to individual by their unique alpha-numeric flag code or color combination.

We visually assessed two measures of body condition for each marked individual: body molt scores (BMS) and abdominal profile indices (API). The BMS is an index between zero and four (with 0.5 increments) based on the amount of alternate plumage present on an individual (e.g., Piersma and Jukema 1993). As body feathers represent up to 75% of total feather mass (Battley and Piersma 1997, 2005) and replacement of these feathers implies a significant metabolic cost associated with feather production and thermoregulation (Klaassen 1995), body molt scores were used as an indicator of individual condition (e.g., Lourenço and Piersma 2015). API is a measure of condition based on the shape of the abdomen and is correlated with actual fat mass in shorebirds (Wiersma and Piersma 1995). Overall flock BMS and API were collected between one and four times per survey (depending on the flock size and the length of the survey) on a total of 1 – 76 individuals (mean = 24 individuals, SD = 14.5) in the flock the marked individual was foraging with. All raw scores were converted to the difference between the average BMS and API of the flock and the marked individual. The residuals from separate regressions of average BMS and API with Julian date were used in analyses as an indicator of condition while controlling for continuous molting and pre-migratory fattening. Lastly, the residuals from a regression of BMS and API were also included as an indicator of condition.

For each marked godwit, we conducted focal foraging observations (n = 87). Using a voice recorder, we dictated observations of godwit behaviors over a five-minute period and later

transcribed recordings using CowLog (Pastell 2016). Because not all focal observations lasted for the full five minutes (e.g., an individual flew out of sight, reshuffled into the foraging flock such that we lost it, or began roosting), we converted the metrics to the number-per-minute-of-observation and eliminated observations that included less than one minute of foraging behaviors. We recorded every behavior of the marked individual, including the number of probes made and the number of prey items captured and consumed (swallowed). We then calculated the number of swallows per minute, the success rate of the focal observation, and the success rate per minute.

We modeled our methodology after the only other non-breeding foraging study of Hudsonian Godwits (Senner and Coddington 2011). We defined a foraging probe as occurring when at least half of an individual's bill was placed in the mud. Godwits frequently probe the mud in rapid succession without removing their bill; in these circumstances, we counted each movement as a separate probe if the bill was lifted one-third of the way out of the mud (Senner and Coddington 2011). We considered a bird to have obtained a prey item when we discerned a swallowing motion or saw an item in its bill. While relatively large and conspicuous Polychaete worms are their primary prey (Ieno et al. 2000), godwits also feed on small items, such as fly larvae (Ribeiro et al. 2004, Senner and Coddington 2011, Walker et al. 2011). Such smaller food items can be consumed without removing the entirety of an individual's bill from the mud and would not have been counted in our swallow or success rate estimates. Consequently, our estimates of foraging success are conservative.

During each survey, we also collected data on predation risk, foraging success, alertness and agitation, human disturbances, land-use of the bay, and foraging substrate availability. These metrics were used to assess patch quality, indicated by flock body condition and godwit density,

in a separate path analysis (see Chapter 4). The scores for flock-averaged body condition and godwit density from the survey associated with our focal individual were used as indicators of patch quality.

For each individual, we averaged each measure across multiple encounters (range: 1 to 7) to derive a single estimation for each variable.

Field Methods – breeding season:

We monitored breeding godwits in 2015 and 2016 in Beluga River, Alaska. Our study area was divided into two study plots of uninterrupted muskeg bog – North (550 ha) and South (120 ha) – that were separated by ~7 km of unmonitored boreal forest and muskeg bog. Both the adjacent tidal mudflats and study plots were surveyed daily for the first two weeks of May to resight returning individuals.

Following this period, we systematically searched plots for nests every two-to-three days throughout the nesting season (May – July). We searched for nests using a combination of prior knowledge, systematic searching, and behavioral observations. Upon discovery of a nest, we recorded a GPS location and floated eggs to estimate the timing of nest initiation, and hence, age of the nest (Liebezeit et al. 2007). We did not physically mark nest locations to minimize the chance of associative learning by predator species (Reynolds 1985). We revisited nests every two-to-three days until either one day prior to the expected hatch or until we observed starred or pipped eggs. Adults were rarely flushed from nests, which were typically checked for incubating birds from 20-30 m away, in an effort to minimize disturbances that might increase the probability of nest failure. Field teams never approached nests directly when predators were observed nearby. A nest was considered successful if ≥1 egg hatched and chicks successfully left

the nest site. Nest failure was presumed when we found empty nests early in the incubation period or destroyed eggs. Due to low rates of nest abandonment in this system (Senner et al. 2017), we considered the failure rate of nests in our study to represent the depredation rate as well.

We then radio-tracked a subset of godwit chicks from successfully hatching nests to assess brood survival. We randomly selected one or two chicks from each brood to receive a small 0.62 g Holohill radio. We clipped the downy feathers from a small area on each chick's back and attached radios above the uropygial gland with cyanoacrylate glue. We deployed up to 20 radios each year, and each chick was located every two-to-three days until the chick had died or fledged. Additionally, we surveyed each plot every two-to-three days for any adult godwit exhibiting defensive behaviors (e.g., perched on a tree, alarm-calling, distraction displays). From this, we determined if at least one chick per brood survived to 20-days-old (yes/no; when radio batteries typically failed), the maximum number of days the brood survived, and the last date an adult was seen defending its brood.

Data Analysis:

Relationships among foraging success, body condition, patch quality, and the breeding performance of godwits were modeled with partial least squares path modeling (PLS-PM). PLS-PM is a type of path analysis, which is a multivariate technique used to explore multiple relationships between blocks of variables and to quantify their respective weights (Lleras 2005, Tenenhaus et al. 2005). This statistical method has only recently been applied to ecological datasets (e.g., Puech et al. 2015), but PLS-PM was selected over covariance-based structural equation modeling approaches primarily because it does not require a large dataset to perform

optimally and because it produces values for each latent variable (Chin and Newsted 1999, Chin 2010).

PLS-PM consists of two sub-models called the inner and the outer model (Sanchez 2013). The outer model describes relationships between a set of observed variables ('manifest variables') and a synthetic 'latent variable' that is built from these manifest variables. A latent variable cannot be measured directly and is representative of a concept (e.g., habitat quality or microclimate). For example, the manifest variables 1) 'swallows per minute', 2) 'success rate of focal observation', and 3) 'success rate per minute' were used to approximate the latent variable 'foraging success'. The group formed by a latent variable and its associated manifest variable(s) is called a block. The inner model describes relationships between latent variables, and relationships are treated as linear regressions. A fitted PLS-PM produces standardized path coefficients for all paths (i.e., direct and indirect effects) that usually range between 0 and ±1. These path coefficients are equivalent to standardized regression coefficients but have the advantage of specifying whether the relationship between latent variables has a positive or negative slope.

Our PLS-PM contained four latent variables (Figures 2 and 3). In the preliminary PLS-PM, all potential manifest variables were included when constructing latent variables. However, before obtaining the final model, we made a set of verifications and transformations, as advised by Sanchez (2013). First, we checked the unidimensionality of each reflective block with Cronbach's alpha and Dillon–Goldstein's rho (Table I). We changed the sign of variables having negative weights to only integrate positively correlated variables in the same block. Then, we examined the loadings – the correlations between a latent variable and its manifest variables (Table II). A manifest variable was only retained if 50% of the variability in the manifest

variable (i.e., factor loading > 0.7) was captured by the latent variable (Sanchez 2013). We retained some individual variables that met unidimensionality but had loadings < 0.7, which we acknowledged as an acceptable trade-off between model quality and meaningfulness. Cross-loadings allowed us to verify if the shared variance within a block was larger than with other blocks and were assessed similarly. Finally, the overall robustness of models was evaluated with the coefficient-of-determination (R^2) and goodness-of-fit (GoF) criterions with a bootstrapping procedure (n = 199). Ninety-five percent confidence intervals that did not encompass zero were considered to imply statistical significance. For PLS-PM, R^2 values for inner models are classified in three categories: low: $R^2 < 0.3$, moderate: $0.3 < R^2 < 0.6$, and high: $R^2 > 0.6$ (Sanchez 2013). The GoF measure assesses the overall predictive performance of both the inner and outer model (Sanchez 2013). Analyses were conducted using the R 3.4.3 software (R Core Development Team 2018) with the 'plspm' package (Sanchez et al. 2017).

Ptilochronology study:

Ptilochronology, or the use of feather growth bars as an index of nutritional condition, has been used extensively since Grubb (1989) first introduced the concept. Feathers have a series of light and dark bands oriented obliquely to the rachis. Each light and dark band taken together (one growth bar) represents 24 hours of growth, and evidence suggests a direct relationship between width of these bars and nutritional condition (Grubb 1989, 1991, Grubb and Cimprich 1990, Grubb and Yosef 1994).

When we captured an individual during the breeding season, we collected the two outermost rectrices to analyze their growth bars (n = 128 feathers from 64 individuals). Because godwit tail feathers are bicolored (black and white), we restricted our ptilochronological

measures to the black portion (farthest from the quill) where growth bars were more easily identified. However, on four feathers, no distinct growth bars could be distinguished. Each feather was scanned into Adobe Lightroom (CS6) and processed until growth bars were visible. Each scan was saved as a jpeg of a standardized size (5 x 4 inches) and number of pixels. The first five growth bars were marked and measured in Adobe Photoshop (CS6) using the 'ruler tool' in number of pixels. We then calculated the mean width of the first five growth bars. Each feather was marked and measured by two observers, and their average measure was used in analyses.

We used generalized linear mixed models with a logistic or poisson regression to examine the influence of non-breeding nutritional condition on nest fate, chick fate, the maximum number of days a chick survived, nest initiation date, and the last date seen defending brood, with individual and year as random effects. We evaluated growth bars in a univariate model against a null model using AIC_C scores for each response variable separately (Burnham and Anderson 2002) with the 'lme4' and 'bbmle' R packages (Bates et al. 2015, Bolker 2017). Lastly, we ran a repeatability analysis on individual growth bar width among years using the rptR package (Stoffel et al. 2017) in program R with 1,000 bootstrap iterations.

One unique aspect of our dataset is that we have direct observations of individuals foraging on the non-breeding grounds for which we also pulled rectrices and indirectly measured nutritional status through feather growth bars. For such linked observations of non-breeding condition, when we have foraging observations and growth bar measures for the same non-breeding season, we also ran a Pearson's correlation matrix to understand the links between our focal foraging observations and growth bar measures.

Results:

Seasonal Survival:

Model selection (Tables III and IV) and estimates of annual survival and resighting probabilities (Table V) differed for the Alaskan and Chilean datasets. Males had a higher annual survival probability than females and model-averaged estimates indicated that survival probabilities were higher in Chile than Alaska. Survival estimates varied among years in the Alaskan dataset, with a noticeable reduction in survival between 2012 and 2015 (Figure 4). In general, resighting probabilities varied among years and were higher in Alaska for both sexes as compared to Chile (Figure 5).

AIC_C ranking of within-season CJS models differed between the Alaskan and Chilean data sets (Tables VI, VII, and VIII). Both analyses, however, clearly indicated that weekly and period survival was high during the stationary breeding and non-breeding periods (Table IX). Males had higher estimated survivorship than females during both stationary periods (Table IX). Resighting probabilities varied across the stationary periods (Table IX).

We estimated weekly survival probability during migration to be 0.986 – 0.993 depending on the annual survival estimate used. Thus, both estimated weekly and period survival rates during migration were lower than during the stationary non-breeding period, but may be higher than during the breeding period, particularly during the short northbound migration (Table X, Figure 6).

Reversible state effects:

Observational study:

From our marked breeding population of ~20 – 30 breeding pairs per year (n = 118

banded adults; n = 496 total banded individuals including chicks), we saw 30 individuals on the non-breeding grounds in 2016 and six individuals in 2015. Eleven individuals were only seen in roosting flocks or were banded as hatch-year chicks and have not been seen on the breeding grounds in subsequent years. Individuals were resighted on anywhere from one to five days in 2016.

The PLS-PM quantified the relative importance of each pathway on future breeding performance of godwits. Based on the fitted PLS-PM (GoF = 0.58), two of our predictors – patch quality and body condition – directly positively affected return rates and breeding performance (Figure 7, Table XI). Both of these latent variables explained ~90% of the total effects on breeding performance (Table XII).

Godwits using higher quality tidal mudflats, as indicated by overall flock density and body condition, had improved foraging success and, ultimately, return rates and breeding performance (Figure 7, Table XII). Successful foragers on the non-breeding grounds were in better condition, and individuals in better condition had better breeding performance (Figure 7, Table XII). In fact, individuals using high quality patches had 47% higher foraging success scores, 57% higher condition scores, and had 77% higher scores for breeding performance. Interestingly, four of the five individuals that did not return to Alaska used lower than average patches, and all five individuals were in poorer than average condition.

Ptilochronology study:

Of the 64 individuals for which we measured growth bars (n = 12, 28, and 24 individuals in 2014, 2015, and 2016 respectively), only two individuals were captured in all three years, and 18 individuals were captured in two years. Growth bar widths within individuals varied among

years (R = 0.09, CI 0, 0.49; p-value = 0.344), indicating changes in nutritional condition among years for an individual.

We found weak evidence that individuals with larger growth bars nested earlier in the year (β = -0.006, CI -0.02, 0.01; Table XIII), had chicks that were more likely to survive to 20-days-old (β = 0.56, CI -0.82, 2.09; Table XIII), hatched broods that were more likely to survive (β = 0.05, CI -0.02, 0.12; Table XIII), and defended broods for longer periods (β = 0.003, CI -0.01, 0.02; Table XIII). We failed to detect a relationship between growth bar width and nest fate, perhaps in part because we had few nest failures represented in our dataset (i.e., 4 of 62 nests). Only 26% (16 of 62) of individuals had broods survive to 20-days-old.

Of the 15 individuals for which we had foraging observations and growth bar measures for the same non-breeding season, we found a strong relationship between growth bar width and API corrected for date of observation (r^2 = 0.76, Table XIV) but not BMS (r^2 = 0.31, Table XIV). Growth bar widths were also related to foraging success: the success rate of the observation (r^2 = 0.51, Table XIV), the success rate per minute (r^2 = 0.50, Table XIV), and the number of swallows per minute (r^2 = 0.50, Table XIV).

Discussion:

Our study is a rare example of how individual performance metrics and seasonal survival estimates can be integrated across the annual cycle for a long-distance migratory species. Adult survival was highest during the stationary non-breeding season but was slightly lower during migration and the breeding season, with the breeding season and southbound migration accounting for the largest proportion of mortality events because of their longer duration and lower survival rates. Furthermore, breeding performance of Hudsonian Godwits was positively

associated with non-breeding season factors, with individuals in better body condition or those that spent time at high quality mudflats during the non-breeding season siring chicks that survived longer. Finally, we found within-individual variation in feather growth bars among years, indicating that conditions on the non-breeding grounds may induce reversible state effects that influence an individual's future breeding performance. The non-breeding season thus likely is a critical period that allows individuals to prepare for future stages of the annual cycle with potentially cascading effects.

Body condition on the non-breeding grounds was positively related to an individual's future breeding performance. Body condition during the non-breeding season may be influenced by habitat quality, prey availability, predation risk, or diet quality (West et al. 2002, Duijns et al. 2009, Sorensen et al. 2009) and is likely critical to the fitness of migratory birds (Bêty et al. 2003, Battley et al. 2004, Bearhop et al. 2004). Both our observational and ptilochronology data corroborated the relationship between body condition during the non-breeding season and future breeding performance. Consistent with previous findings (Chapter 4), our data suggest that foraging success rates largely drove non-breeding season body condition. Low rates of energy intake prior to migration and/or breeding can adversely affect reproduction (Ebbinge and Spaans 1995, Gill et al. 2001, Prop et al. 2003). Pre-migratory fueling substantially increases daily energy needs and may require extending periods of foraging and/or increasing the rate of energy intake (Blem 1980, Duijns et al. 2009). Moreover, patch quality affected foraging success directly and body condition indirectly. Intertidal mudflats may vary in prey availability or capture efficiencies, which then affects an individual's foraging success and ultimately body condition. As such, the ability of birds to sufficiently refuel prior to migration may reflect differences in patch quality and foraging success among tidal mudflats.

We also found evidence for important links between habitat quality in the non-breeding season and an individual's subsequent reproductive success. The quality of mudflats, as indicated by flock condition and density was a function of the availability of foraging habitat, foraging success (likely a proxy for prey availability), and number of disturbances. Mudflat quality was, in turn, positively associated with return rates to the breeding grounds and reproductive success. As such, our measure of patch quality supports the idea that the reversible state effects we documented were not driven exclusively by intrinsic variation among individuals, but also by habitat conditions that presumably affected entire flocks. As described in Chapter 4, mudflats in the Chiloé region vary widely in terms of both the type and intensity of human disturbances, which reduce foraging time and/or increase energy expenditure (through displacement flights) in ways that appear to reduce individual condition.

An important caveat of our work is that we could not perfectly determine the quality of all habitats used by an individual during the non-breeding season because individuals likely used multiple bays and mudflats. Although the degree to which godwits move among tidal mudflats is unknown, our observations suggest that it is relatively common. Of the 20 individuals we saw multiple times in 2016, only five individuals were seen in a single location. The remaining 15 individuals were observed at two to three different sites that were separated by distances ranging from 3 – 40 km (μ = 14.9, sd = 14.4). That said, most individuals were restricted to sub-regions within the greater Chiloé Island area – restricting their movements to either the northern coastline (e.g., Quetalmahue and Caulín) or the Castro region (e.g., Pullao, Chúllec, Nercón). Whether our estimates of habitat quality are representative of the entire non-breeding season is unknown and requires further detailed study into the small-scale movements of individuals.

Although we determined that survival was highest during the non-breeding stationary period, we were unable to precisely differentiate survival rates between breeding and migratory periods. Migration is often considered to be the most taxing part of the migratory annual cycle due to the large distances moved, threats faced (e.g., severe weather), and unfamiliarity of stopover locations. For many species, migration is the period with lowest survival (Sillett and Holmes 2002, Klaassen et al. 2014, Lok et al. 2015, Rockwell et al. 2017). However, work with extreme long-distance birds has shown a pattern of higher survival during migration than other periods of the annual cycle (Leyrer et al. 2013, Rakhimberdiev et al. 2015, Senner et al. in review). For instance, Bar-tailed (*Limosa lapponica*) and Hudsonian Godwits both demonstrate high adult survival, little evidence for elevated migration mortality, no apparent minimization of non-stop flight distances, and low inter- and intra-individual variation in migratory performance (Conklin et al. 2017). Our results support this pattern, with high survival rates observed throughout the annual cycle and seasonal survival potentially being the lowest during the breeding season. High breeding season mortality is likely a combination of high predation risk compared to the rest of the annual cycle, as well as high energetic demands (Drent and Daan 1980). Interestingly, females had lower survival estimates in all of our analyses potentially due to the increased costs of egg-laying and diurnal incubation. In fact, all of the known adult mortalities documented in seven years of monitoring breeding godwits were incubating females. Although individuals may be able to compensate for this risk by choosing to nest within a protective nesting association (Swift et al. 2018, Chapter 3), the relatively low annual and breeding season survival estimates for females indicate that reproduction may be costly for godwits.

Our data suggests that individuals in better body condition during the previous non-breeding season had subsequently improved breeding performance. Individuals observed on the non-breeding grounds in better body condition were more likely to return to Alaska and had better nest and brood survival. Similarly, individuals in better nutritional condition during the previous non-breeding season had higher chick survival. However, on the breeding grounds godwits nest within and outside of a protective nesting association with Mew Gulls, where individuals within gull colonies have improved nest survival but reduced brood survival (Swift et al. 2018). Of the 25 individuals tracked in our observation based study, 16 nested within the gull colony (64%) which is lower than the average amount of the population that nest within the gull colony (73%). Therefore, our observational study is representative of the entire breeding population nesting within and outside of the Mew Gull colony.

Contrary to our detection of reversible state effects on breeding performance mediated through body condition, Senner et al. (2014) found that returning godwits that migrated later than the population mean during one portion of their annual cycle did not continue to migrate later than the population mean for the entirety of their annual cycle, nor did individual's suffer reduced breeding success or survival as a result of delayed arrivals at breeding sites. Our detection of reversible state effects in Hudsonian Godwits differs from previous work on this breeding population and may be explained by two non-mutually exclusive hypotheses. First, the current study focuses on body condition rather than the timing of migration, the latter of which may be more consistent within an individual than condition (Prop et al. 2003). As such, the two apparently contrasting results may be co-occurring. Alternatively, the detection of condition-mediated reversible state effects may indicate a shift in the resources or threats facing godwits between the previous study (2009 – 2012) and the current one (2015 – 2016). Therefore, though

timing of events during the annual cycle may show no effects on survival or future breeding performance of godwits, individuals in better body condition during the non-breeding season have improved return rates and subsequent breeding performance.

Links between non-breeding ecology and subsequent breeding performance may reflect reversible state effects from the non-breeding to breeding season or individuals of differing quality. Costs of migration may disproportionately affect some individuals based on their relative condition or quality (Senner et al. 2015, Conklin et al. 2017). The apparent absence of a strong influence of timing delays on reproductive success suggests that strong selection has constrained the timing of migration and similar patterns are found in other extreme long distance migrants (Conklin and Battley 2012, Senner et al. 2014, Conklin et al. 2017). Individuals may continue to migrate at the same time as the rest of the population, especially on northbound migration, even if they are in poorer body condition (e.g., Ebbinge and Spaans 1995, Prop et al. 2003). As such, the positive reversible state effect we detected might reflect differences in individual quality with some individuals failing to meet a threshold to maintain their annual cycle strategy effectively. Though this possibility cannot be eliminated without repeat observations of individuals across years in our observational study, the annual variation in growth bars across our three-year dataset suggests that certain individuals may not be inherently of higher quality and that nutritional condition is in fact a reversible trait. Moreover, the apparent influence of habitat quality, as indicated by the qualities of the entire foraging flock, provides additional evidence that conditions on the non-breeding grounds may affect individual body condition beyond intrinsic or genetic effects. In long-distance migrants, variation in individual quality may result in differences that accrue across the annual cycle, but changes in individual condition among years

suggests that condition may indirectly influence future reproductive success through reversible state effects.

Our data suggest that godwit annual survival has been declining across a period of several years in the Alaskan breeding population, suggesting a regime shift in either resource availability or the occurrence of the anthropogenic threats. Although the cause of this decline is unknown, our data corroborates steep declines observed in all three breeding populations at stopover sites during southward migration (Smith et al. unpubl. data). This decline in survival and population size coincides with the period during which we were able to simultaneously monitor godwits during both the non-breeding and breeding seasons and during which we found evidence of reversible state effects. Thus, one potential reason that previous studies in this system (e.g., Senner et al. 2014) had not detected reversible state effects, but our current study did, is that conditions have changed such that godwits now face a bottleneck either during the non-breeding season or northward migration. In this way, the correlation between non-breeding season body condition and future breeding performance may suggest that more recent within-season survival estimates on the non-breeding grounds may have declined from our estimates. Thus, the reversible state effects detected could instead indicate a continued narrowing of the individual quality spectrum that can continue to maintain such an extreme migration strategy or the degradation of resources necessary for individuals to do so.

Our study provides evidence for positive reversible state effects of non-breeding season body condition on Hudsonian Godwits future breeding performance. The mudflats used throughout the non-breeding season also positively influenced breeding performance, and an individual's foraging success improved their body condition. Further, body condition, measured both directly and indirectly, strongly influenced future chick survival. The reversible state effect

detected aligned with a period of low annual survival, as measured on the breeding grounds, and may indicate that godwits now face a bottleneck either during the non-breeding season or northward migration. Using this rare dataset of individually-linked observations of cross-season performance and demography enabled us to identify that reversible state effects were acting across non-breeding to breeding seasons and that they influenced variation in seasonal survival rates. Further studies of long-distance migratory species should continue to connect measures of individual performance (i.e., reversible state effects) to demographic survival studies so as to enable us to identify when bottlenecks occur during the annual cycle, as well as their underlying causes, and helping to inform conservation actions.

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The authors declare that they have no conflict of interest.

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TABLES AND FIGURES

Table I. The outer model fit of the fitted partial least squares path model. Weight indicates the weighting used in the outer model. The Cronbach's alpha is a coefficient that is intended to evaluate how well a block of indicators measures their corresponding latent construct with values greater than 0.7 considered acceptable. The Dillon-Goldstein's rho focuses on the variance of the sum of variables in the block of interest, with a block considered as unidimensional when the Dillon-Goldstein's rho is larger than 0.7. Lastly, if a block is unidimensional, the first eigenvalue should be "much more" larger than 1, whereas the second eigenvalue should be smaller than 1.

	Cronbach's alpha	Dillon-Goldstein's rho	1st Eigenvalue	2nd Eigenvalue
Foraging Success	0.95	0.97	2.73	0.25
Body Condition	0.86	0.91	2.85	0.69
Patch Quality	0.77	0.90	1.62	0.38
Breeding Performance	0.82	0.88	2.60	0.92

Table II. Outer model output of the fitted partial least squares path model. Weight indicates the weighting used in the outer model. Loadings are the correlations between a latent variable and its indicators. Communalities are the squared loading values and indicate the amount of variability explained by a latent variable.

	weight	loading	communality
Foraging Success			
Success rate	0.36	0.98	0.97
Swallows per min	0.32	0.91	0.82
Success rate per min	0.37	0.97	0.94
Body Condition			
Condition residuals	0.48	0.93	0.87
Body molt score	0.29	0.76	0.57
Abdominal profile index	0.38	0.86	0.73
Patch Quality			
Density scores	0.57	0.91	0.82
Condition scores	0.54	0.89	0.80
Breeding Performance			
Returned	0.55	0.89	0.79
Nest fate	0.32	0.88	0.77
Chick fate	0.08	0.53	0.28
Maximum chick days	0.25	0.76	0.58

Table III. Summary of competing models evaluating Hudsonian Godwit (*Limosa haemastica*) annual survival on the breeding grounds at Beluga River, Alaska. Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for all adult godwits banded and resighted from 2009 – 2017.

Model	$dAIC_C$	k	weight
Phi(year) p(constant)	**0.00**	**8**	**0.31**
Phi(constant) p(year)	**0.06**	**8**	**0.30**
Phi(sex) p(year)	**0.90**	**9**	**0.20**
Phi(year) p(sex)	2.04	9	0.11
Phi(year) p(year)	4.04	14	0.04
Phi(year * sex) p(constant)	5.60	15	0.02
Phi(year * sex) p(sex)	7.64	16	0.01
Phi(constant) p(constant)	9.26	2	0.00
Phi(sex) p(constant)	9.67	3	0.00
Phi(year * sex) p(year)	10.27	21	0.00
Phi(constant) p(sex)	11.29	3	0.00
Phi(sex) p(sex)	11.65	4	0.00
Phi(constant) p(year * sex)	12.96	15	0.00
Phi(sex) p(year * sex)	14.27	16	0.00
Phi(year) p(year * sex)	17.23	21	0.00
Phi(year * sex) p(year * sex)	25.34	28	0.00

Table IV. Summary of competing models evaluating Hudsonian Godwit (*Limosa haemastica*) annual survival on the non-breeding grounds near Chiloé Island, Chile. Models are ranked by ascending adjusted $dQAIC_C$ values with the number of parameters (k), and Akaike weights for all adult godwits banded and resighted from 2007 – 2012.

Model	$dQAIC_C$	k	weight
Phi(constant) p(year)	**0.00**	**6**	**0.66**
Phi(sex) p(year)	**1.56**	**7**	**0.30**
Phi(year) p(year)	6.56	10	0.02
Phi(constant) p(year * sex)	9.16	11	0.01
Phi(sex) p(year * sex)	11.10	12	0.00
Phi(year * sex) p(year)	11.74	15	0.00
Phi(year) p(year * sex)	15.80	15	0.00
Phi(year * sex) p(year * sex)	21.09	20	0.00
Phi(year) p(constant)	74.43	6	0.00
Phi(year) p(sex)	76.26	7	0.00
Phi(year * sex) p(constant)	79.33	11	0.00
Phi(year * sex) p(sex)	81.35	12	0.00
Phi(constant) p(constant)	112.27	2	0.00
Phi(sex) p(constant)	114.24	3	0.00
Phi(constant) p(sex)	114.25	3	0.00
Phi(sex) p(sex)	116.24	4	0.00

Table V. Model averaged estimates of annual survival (φ) and resighting (p) probabilities and 95% confidence intervals (CI) for Hudsonian Godwits (*Limosa haemastica*) from Beluga River, Alaska, USA (2009 – 2017) and Chiloé Island, Chile (2007 – 2012).

Location	φ	(95% CI)	p	(95% CI)
Alaska	0.740	(0.582, 0.855)	0.953	(0.740, 0.995)
Male	0.747	(0.587, 0.860)	-	-
Female	0.734	(0.577, 0.849)	-	-
Chile	0.821	(0.783, 0.853)	0.537	(0.450, 0.620)
Male	0.824	(0.786, 0.856)	-	-
Female	0.818	(0.780, 0.853)	-	-

Table VI. Summary of competing models evaluating Hudsonian Godwit (*Limosa haemastica*) within season survival on the breeding grounds in Beluga River, Alaska. Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights for all adult godwits seen during each breeding season from 2009 – 2016.

Model	$dAIC_C$	k	weight
Phi(sex) p(time)	**0.00**	**7**	**0.62**
Phi(constant) p(time)	**1.36**	**6**	**0.31**
Phi(time) p(time)	4.41	10	0.07
Phi(time) p(constant)	54.39	6	0.00
Phi(time) p(sex)	55.09	7	0.00
Phi(sex) p(sex)	66.42	4	0.00
Phi(sex) p(constant)	66.93	3	0.00
Phi(constant) p(constant)	70.36	2	0.00
Phi(constant) p(sex)	71.32	3	0.00

Table VII. Summary of competing models evaluating Hudsonian Godwit (*Limosa haemastica*) within season survival on the non-breeding grounds near Chiloé Island, Chile. Models are ranked by ascending adjusted $dAIC_C$ values with the number of parameters (k), and Akaike weights for all adult godwits seen during the 2009 – 2010 non-breeding season.

Model	$dAIC_C$	k	weight
Phi(sex) p(time)	**0.00**	**5**	**0.52**
Phi(constant) p(time)	**0.35**	**4**	**0.43**
Phi(time) p(time)	4.73	6	0.05
Phi(constant) p(sex)	27.81	3	0.00
Phi(constant) p(constant)	29.33	2	0.00
Phi(time) p(sex)	29.59	5	0.00
Phi(sex) p(sex)	29.87	4	0.00
Phi(sex) p(constant)	31.37	3	0.00
Phi(time) p(constant)	33.44	4	0.00

Table VIII. Summary of competing models evaluating Hudsonian Godwit (*Limosa haemastica*) within season survival on the non-breeding grounds near Chiloé Island, Chile. Models are ranked by ascending adjusted $dQAIC_C$ values with the number of parameters (k), and Akaike weights for all adult godwits seen during the 2010 – 2011 non-breeding season.

Model	$dQAIC_C$	k	weight
Phi(constant) p(sex)	**0.00**	**3**	**0.48**
Phi(sex) p(sex)	**1.06**	**4**	**0.28**
Phi(constant) p(constant)	3.09	2	0.10
Phi(time) p(sex)	4.08	5	0.06
Phi(sex) p(constant)	5.11	3	0.03
Phi(constant) p(time)	6.85	4	0.01
Phi(time) p(constant)	7.15	4	0.01
Phi(time) p(time)	9.01	6	0.00
Phi(sex) p(time)	-	-	-

Table VIX: Model averaged estimates of within season survival (φ) and resighting (p) probabilities and 95% confidence intervals (CI) for Hudsonian Godwits (*Limosa haemastica*) from Beluga River, Alaska, USA (2009 – 2016) and Chiloé Island, Chile (2010 – 2011).

Location	φ	(95% CI)	p	(95% CI)
Alaska	0.960	(0.929, 0.978)	0.778	(0.678, 0.838)
Male	0.969	(0.936, 0.986)	-	-
Female	0.951	(0.921, 0.970)	-	-
Chile	0.999	(0.998, 0.999)	0.702	(0.635, 0.764)
Male	0.999	(0.998, 0.999)	-	-
Female	0.999	(0.998, 0.999)	-	-

Table X. Estimates of seasonal survival, period length, and weekly survival estimates for Hudsonian Godwits (*Limosa haemastica*) from Beluga River, Alaska, USA and Chiloé Island, Chile.

	Southbound Migration	Non-breeding	Northbound Migration	Breeding
Weekly survival	0.986 – 0.993	0.999	0.986 – 0.993	0.992
Period length	~11 weeks	27 weeks	~3 weeks	11 weeks
Period survival	0.855 – 0.928	0.987	0.958 – 0.979	0.915

Table XI. Results of bootstrapping procedure of the fitted partial least squares path model for Hudsonian Godwit (*Limosa haemastica*) reversible state effects. Significant paths, where 95% confidence intervals (CI) did not cross 0, are bolded.

	Beta	95% CI
Patch Quality -> Foraging Success	**0.59**	**(0.27, 0.77)**
Patch Quality -> Body Condition	0.09	(-0.17, 0.42)
Patch Quality -> Breeding Performance	**0.47**	**(0.06, 0.91)**
Foraging Success -> Body Condition	**0.68**	**(0.38, 0.98)**
Foraging Success -> Breeding Performance	-0.19	(-0.61, 0.27)
Body Condition -> Breeding Performance	**0.48**	**(0.14, 0.87)**

Table XII. The relative contribution of direct and indirect effects (calculated from standardized path coefficients) and the total effect for each path in the fitted partial least squares path model for Hudsonian Godwit (*Limosa haemastica*) reversible state effeccts. Paths connect latent variables.

	direct	indirect	total
Patch Quality -> Foraging Success	0.58	0.00	0.58
Patch Quality -> Body Condition	0.10	0.40	0.50
Patch Quality -> Breeding Performance	0.50	0.10	0.60
Foraging Success -> Body Condition	0.68	0.00	0.68
Foraging Success -> Breeding Performance	-0.20	0.33	0.13
Body Condition -> Breeding Performance	0.48	0.00	0.48

Table XIII. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) reproductive success and average growth bar width of outermost rectrices, indicating non-breeding season nutritional condition, of godwits captured on nests at Beluga River, Alaska in 2014 – 2016. Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights.

Model	$dAIC_C$	k	Weight
Nest Fate			
Null (Individual + Year random effect)	0.00	3	0.74
Average growth bar width	2.10	4	0.26
Chick Survival to 20-days-old			
Average growth bar width	0.00	4	0.93
Null (Individual + Year random effect)	5.10	3	0.07
Nest Initiation Date			
Average growth bar width	0.00	4	0.99
Null (Individual + Year random effect)	11.4	3	0.01
Maximum number of days a chick survived			
Average growth bar width	0.00	4	1.0
Null (Individual + Year random effect)	19.5	3	<0.001
Last date defending brood			
Average growth bar width	0.00	4	0.99
Null (Individual + Year random effect)	12.4	3	0.01

Table XIV. Pearson correlation coefficients for linked non-breeding season observations and feather data for Hudsonian Godwits (*Limosa haemastica*). Body molt score (BMS) and abdominal profile index (API) are corrected for date of observation.

	Non-breeding season observed body condition			Non-breeding season observed foraging success			Feather Data		
	Condition Residuals	BMS	API	Success Rate	Swallows per min	Success Rate per min	Average Growth Bar Width	Feather Mass	Feather Length
Average Growth Bar Width	0.26	0.31	0.76	0.51	0.49	0.50	1		
Feather Mass	0.18	0.16	0.07	-0.06	0.09	-0.06	0.12	1	
Feather Length	0.34	0.29	0.18	0.25	0.18	0.30	0.24	0.61	1

Figure 1. Locations of study areas in Beluga River, Alaska, USA and Chiloé Island, Chile and months in the annual cycle when Hudsonian Godwits (*Limosa haemastica*) are present at each location.

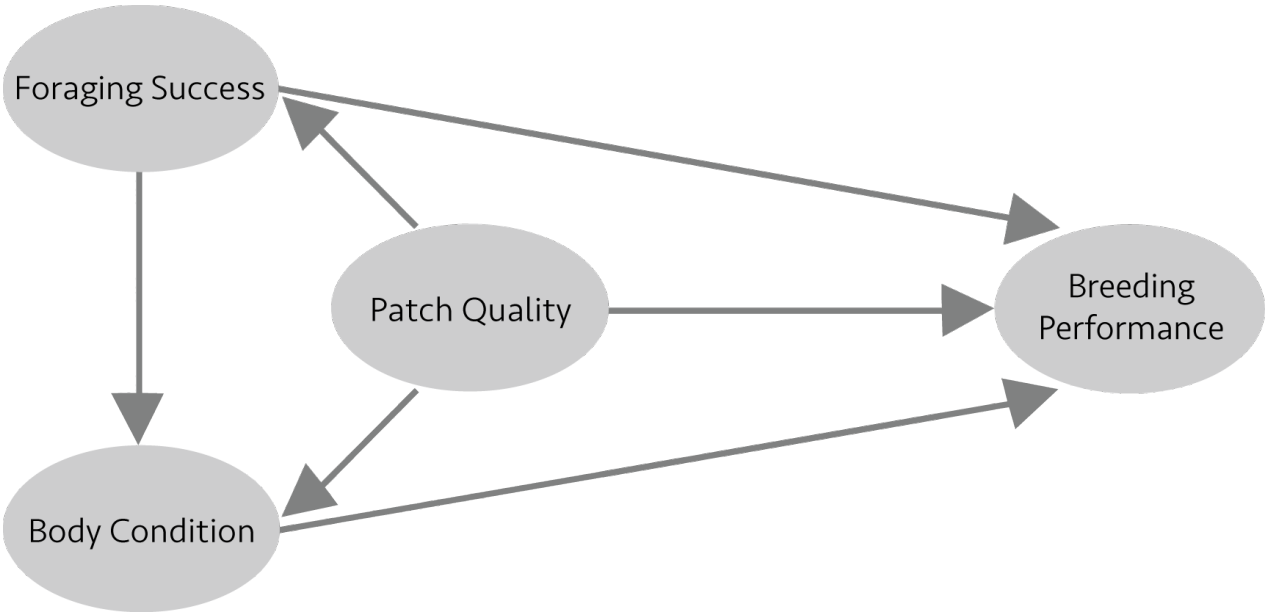

Figure 2. The partial least squares inner path model for Hudsonian Godwit (*Limosa haemastica*) reversible state effects. Ovals represent each of the 'latent' variables with the proposed relationships between each latent variable shown by the dark gray arrows.

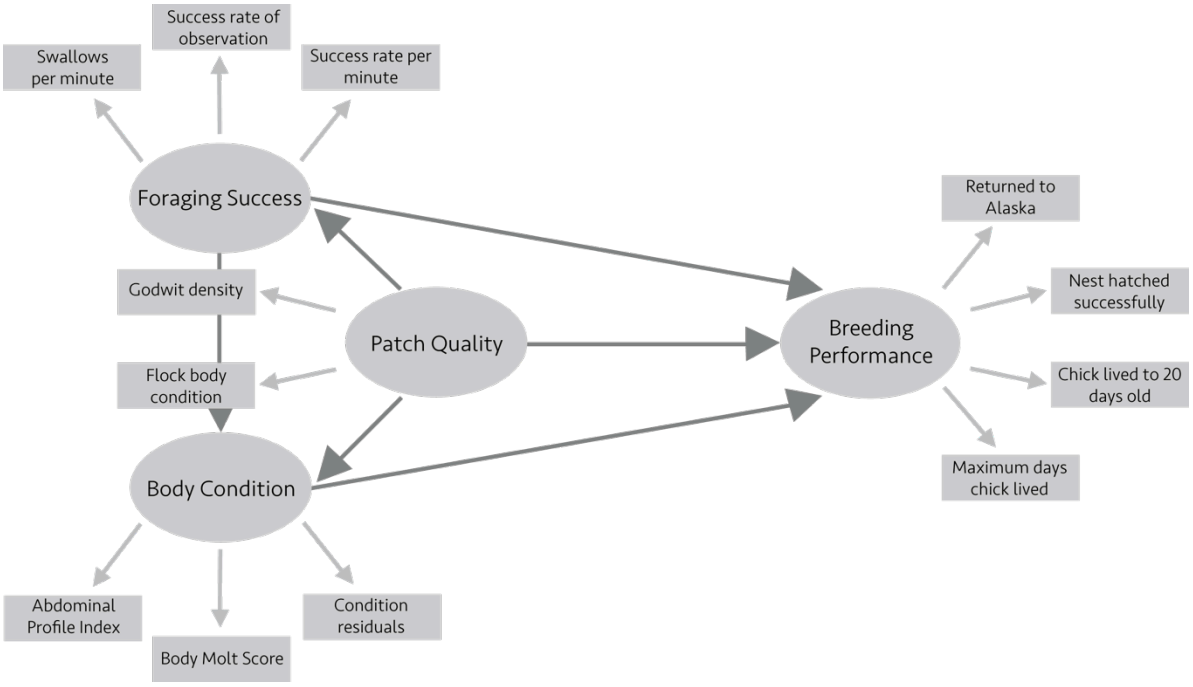

Figure 3. The final partial least squares path model for Hudsonian Godwit (*Limosa haemastica*) reversible state effects. 'Manifest' variables are shown in rectangles and 'latent' variables in ovals. The light gray arrows show the link between the manifest variables and each latent variable. The inner model describing the relationships between the latent variables is represented using dark gray arrows.

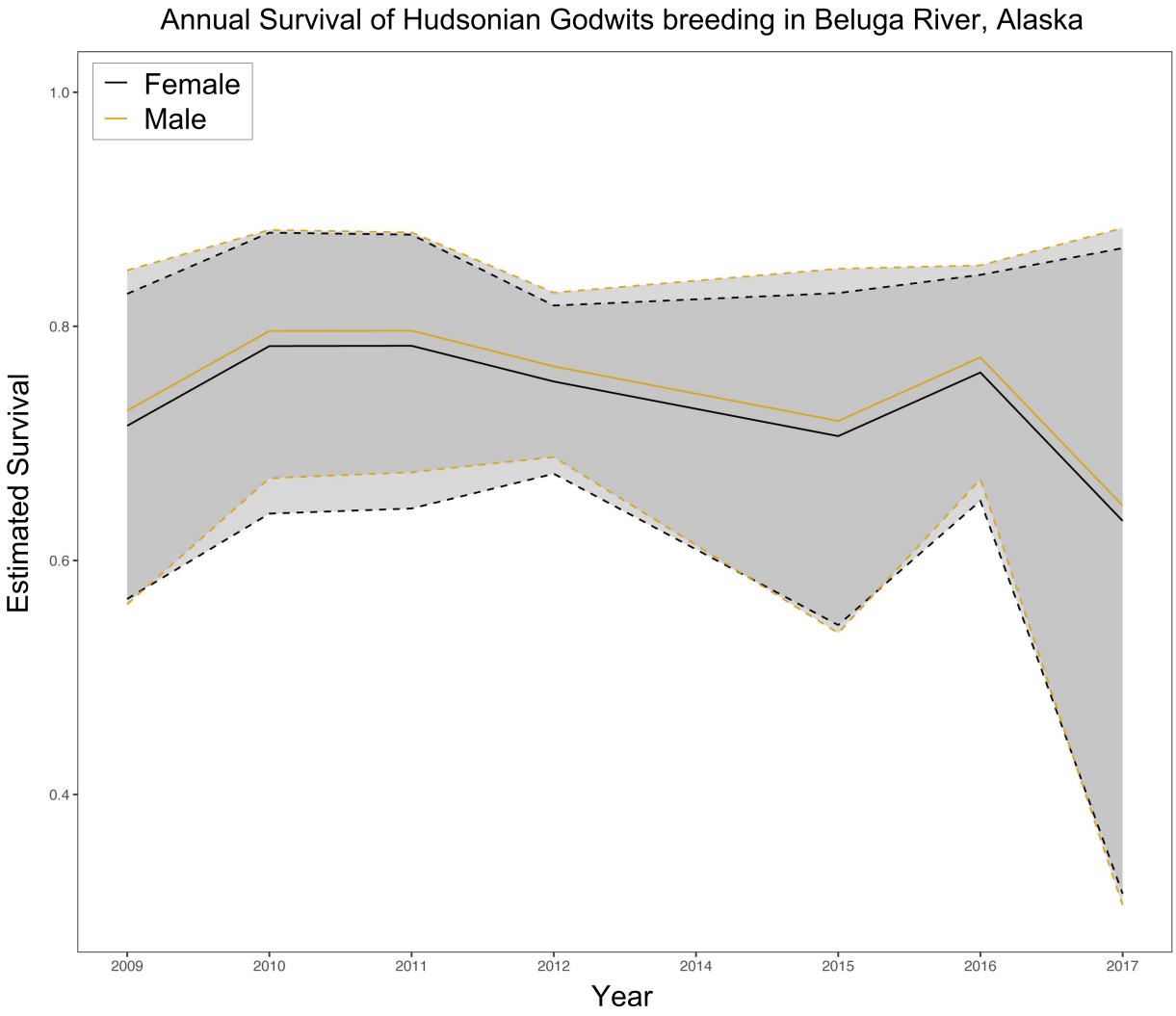

Figure 4. Annual survival estimates of Hudsonian Godwits (*Limosa haemastica*) from the breeding grounds at Beluga River, Alaska, USA from 2009 to 2017 (minus 2013). Sex-specific estimates (male: yellow; female: black) and 95% confidence intervals shown (dashed lines and gray areas).

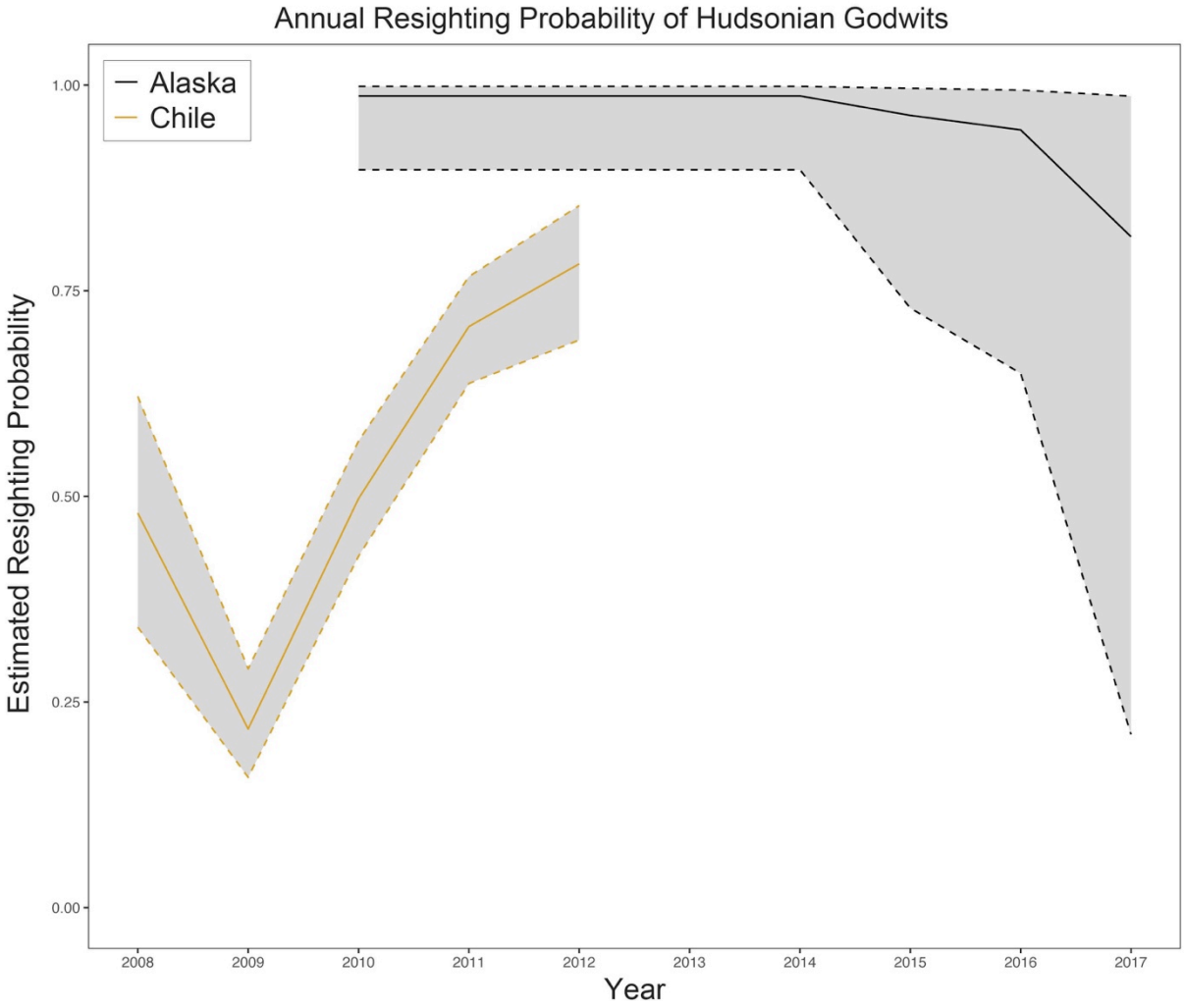

Figure 5. Annual resighting probability of Hudsonian Godwits (*Limosa haemastica*) on the breeding grounds at Beluga River, Alaska, USA (black) and non-breeding grounds on Chiloé Island, Chile (yellow). Estimates and 95% confidence intervals shown (dashed lines and gray areas).

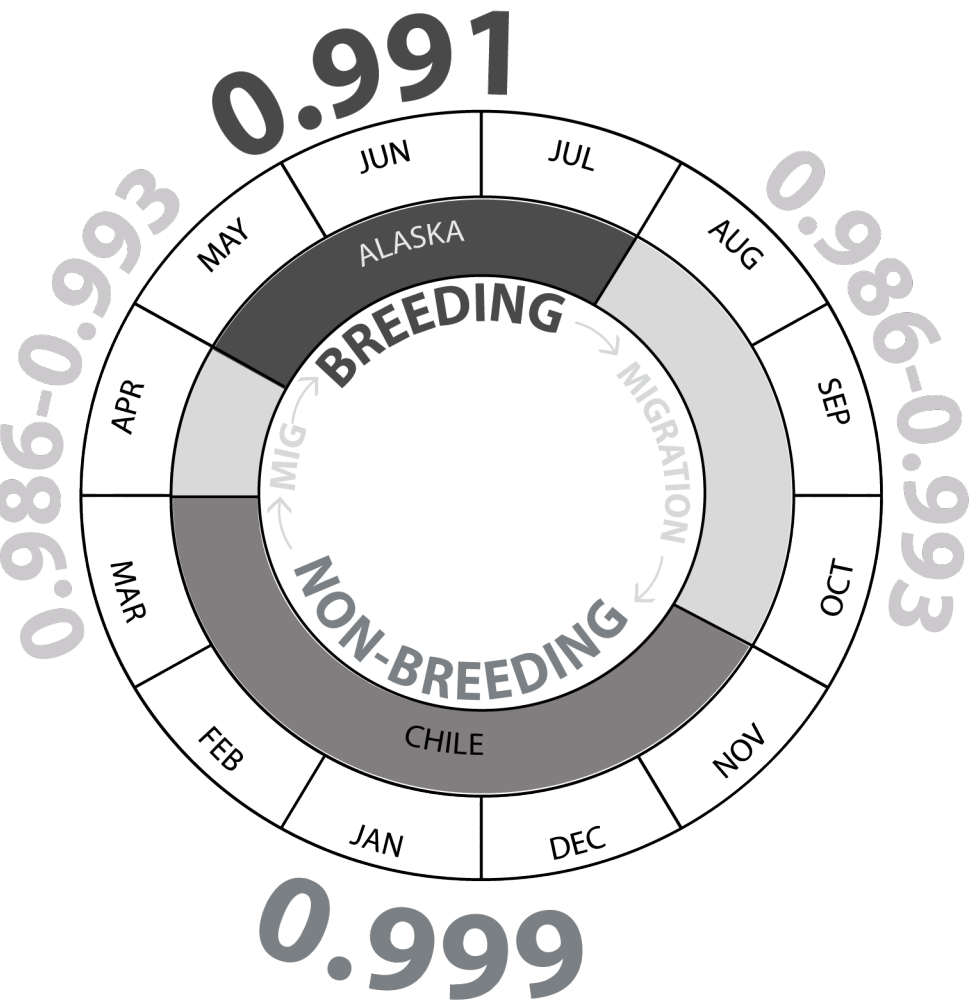

Figure 6. Weekly survival estimates for the four seasonal intervals in the annual cycle of Hudsonian Godwits (*Limosa haemastica*). Breeding season survival May–July (11 weeks), non-breeding season survival October–March (27 weeks), and the two migration intervals represent survival during the 14-week northbound and southbound migration periods of unequal lengths. Within breeding season survival estimates are from 2009 – 2016 at Beluga River, Alaska, USA. Within non-breeding season survival estimates are from 2009 – 2010 and 2010 – 2011 on Chiloé Island, Chile.

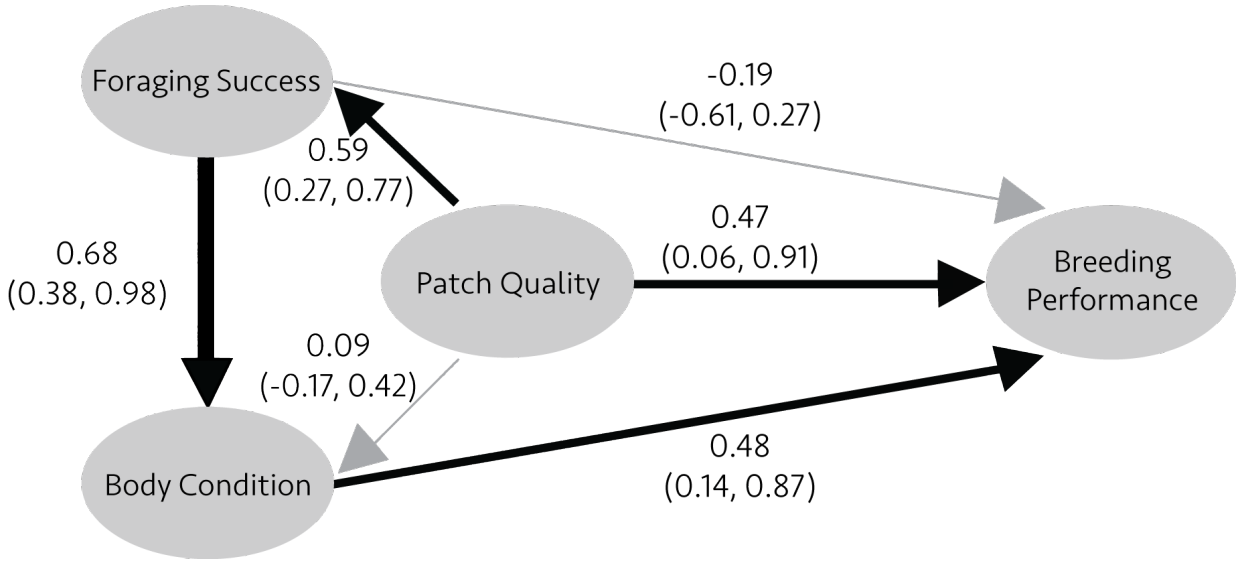

Figure 7. Partial least squares path diagram of both direct and indirect effects on future breeding performance of Hudsonian Godwits (*Limosa haemastica*). Arrows point from predictor to response variables within the model and the thickness of the arrows is proportional to the respective path values (mean bootstrapped standardized path coefficients). Black lines represent significant relationships while gray lines represent non-significant relationships based on 199 bootstrapped iterations. Coefficients of determination (R^2) and 95% confidence intervals are reported for response variables within the model.

APPENDIX F

Methods:

Feathers may also be shorter and lighter under nutritional stress conditions, when allocation of resources to plumage production may be limited (Murphy et al. 1988, Carbonell and Tellería 1999). Feather stiffness and hardness may be positively correlated with feather mass (Dawson et al. 2000), so feather mass could be an indirect measure of feather quality. One cost of having shorter and lighter feathers may be an impaired flight performance, which could affect foraging efficiency and increase predation risk (Slagsvold and Dale 1996). Also, lower-quality feathers might influence migration speed, prolonging the duration of migration (Marchetti et al. 1995, Hedenström and Alerstam 1998).

Feather mass:

For each outer rectrix pulled from incubating individuals (n = 128 feathers from 64 individuals), we weighed and measured the full length of the feather. Using a Mettler Toledo New Classic MF balance (MS802S), we weighed each feather (g) twice. The calibration of the scale was checked every tenth feather. Using calipers, we measured the full length of the barbed portion of the feather (mm) twice. The residuals from a regression of feather mass and length were used as an indicator of feather quality.

Data analysis:

We used generalized linear mixed models with a logistic or poisson regression to examine the influence of non-breeding feather quality on nest fate, chick fate, the maximum number of days a chick survived, nest initiation date, and the last date seen defending brood,

with individual and year as random effects. We evaluated feather quality in a univariate model to a null model using AIC_C scores for each response variable separately (Burnham and Anderson 2002) in program R (R Core Development Team 2018) with the 'lme4' and 'bbmle' packages (Bates et al. 2015, Bolker 2017). Lastly, we ran a repeatability analysis on individual feather mass and length among years using the rptR package (Stoffel et al. 2017) in program R with 1,000 bootstrap iterations.

For linked observations of non-breeding condition, when we have foraging observations and growth bar measures for the same non-breeding season, we ran a Pearson's correlation matrix to understand the links between our focal foraging observations and growth bar measures.

Results:

Breeding performance was not explained by feather quality (Table FI). Feather mass and length were both highly repeatable among years (Mass: R = 0.79, CI 0.57, 0.91, p-value < 0.001; Length: R = 0.95, CI 0.89, 0.98, p-value < 0.001).

Of the 15 individuals for which we have foraging observations and feather measures for the same non-breeding season, we found no relationships between feather mass or length with either foraging success or body condition measures.

Discussion:

Tail feather mass and length were highly repeatable among years, but feather growth rate was not repeatable, which suggests that the latter trait mainly indicates environmental circumstances during molt, whereas feather mass and length may more strongly reflect structural or genetic effects. As godwits have an extended period to molt, feather quality may be highly

constrained. Similar patterns of constrained molt strategies are seen in other long distance migrants (Hargitai et al. 2014, Conklin and Battley 2012).

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TABLES AND FIGURES

Table FI. Summary of competing models evaluating relationships between Hudsonian Godwit (*Limosa haemastica*) reproductive success and the residuals from a regression of feather mass and length, indicating feather quality, of godwits captured on nests at Beluga River, Alaska in 2014 – 2016. Models are ranked by ascending $dAIC_C$ values with the number of parameters (k), and Akaike weights.

Model	$dAIC_C$	k	Weight
Nest Fate			
Null (Individual + Year random effect)	0.00	3	0.74
Mass regression	2.10	4	0.26
Chick survival to 20-days-old			
Null (Individual + Year random effect)	0.00	3	0.63
Mass regression	1.10	4	0.37
Nest initiation date			
Null (Individual + Year random effect)	0.00	3	0.73
Mass regression	1.90	4	0.27
Maximum number of days brood survived			
Null (Individual + Year random effect)	0.00	3	0.73
Mass regression	2.00	4	0.27
Last date defending brood			
Null (Individual + Year random effect)	0.00	3	0.72
Mass regression	1.90	4	0.28

APPENDIX G

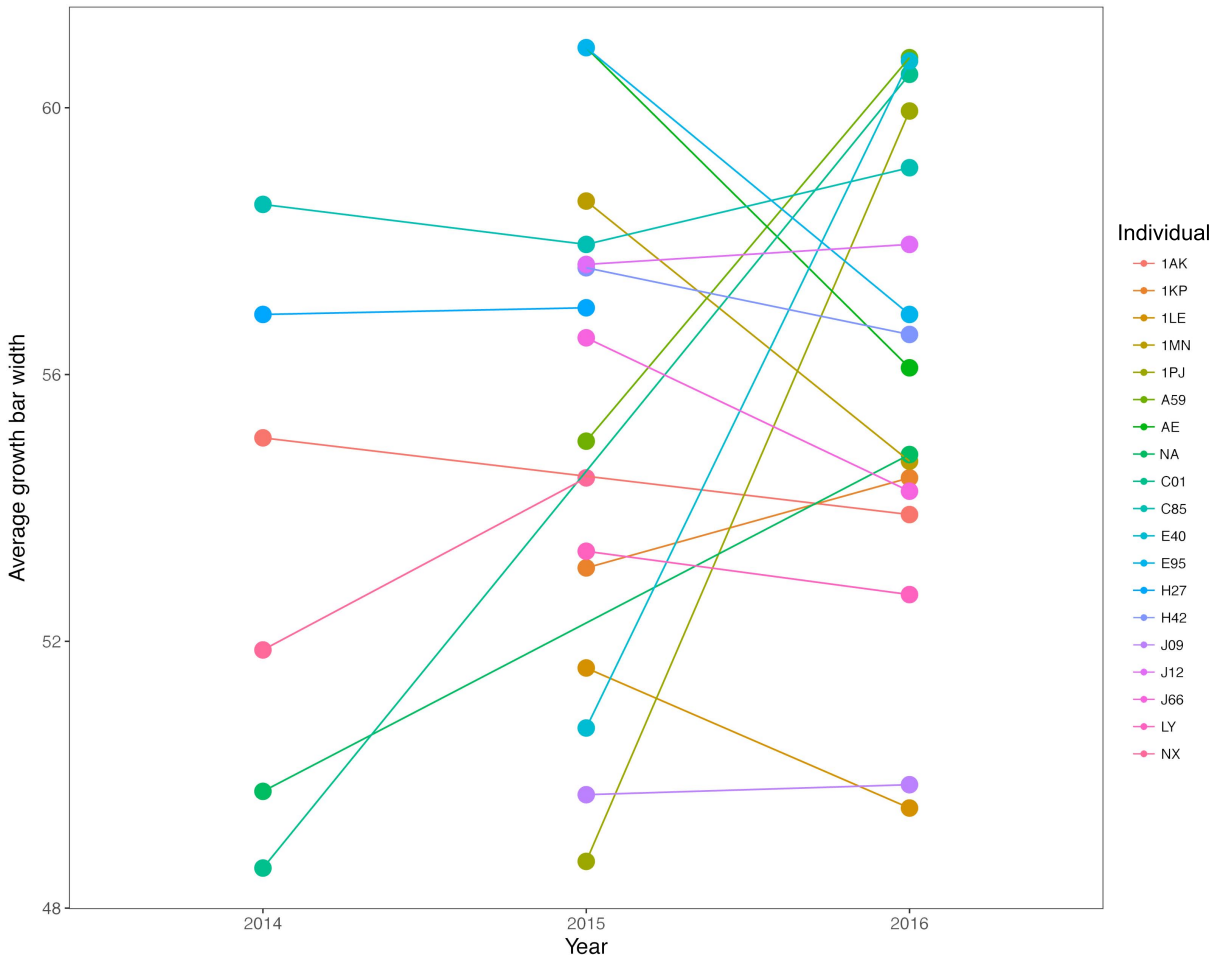

Figure G1. Average growth bar width varied among years for individual Hudsonian Godwits (*Limosa haemastica*) breeding at Beluga River, Alaska.

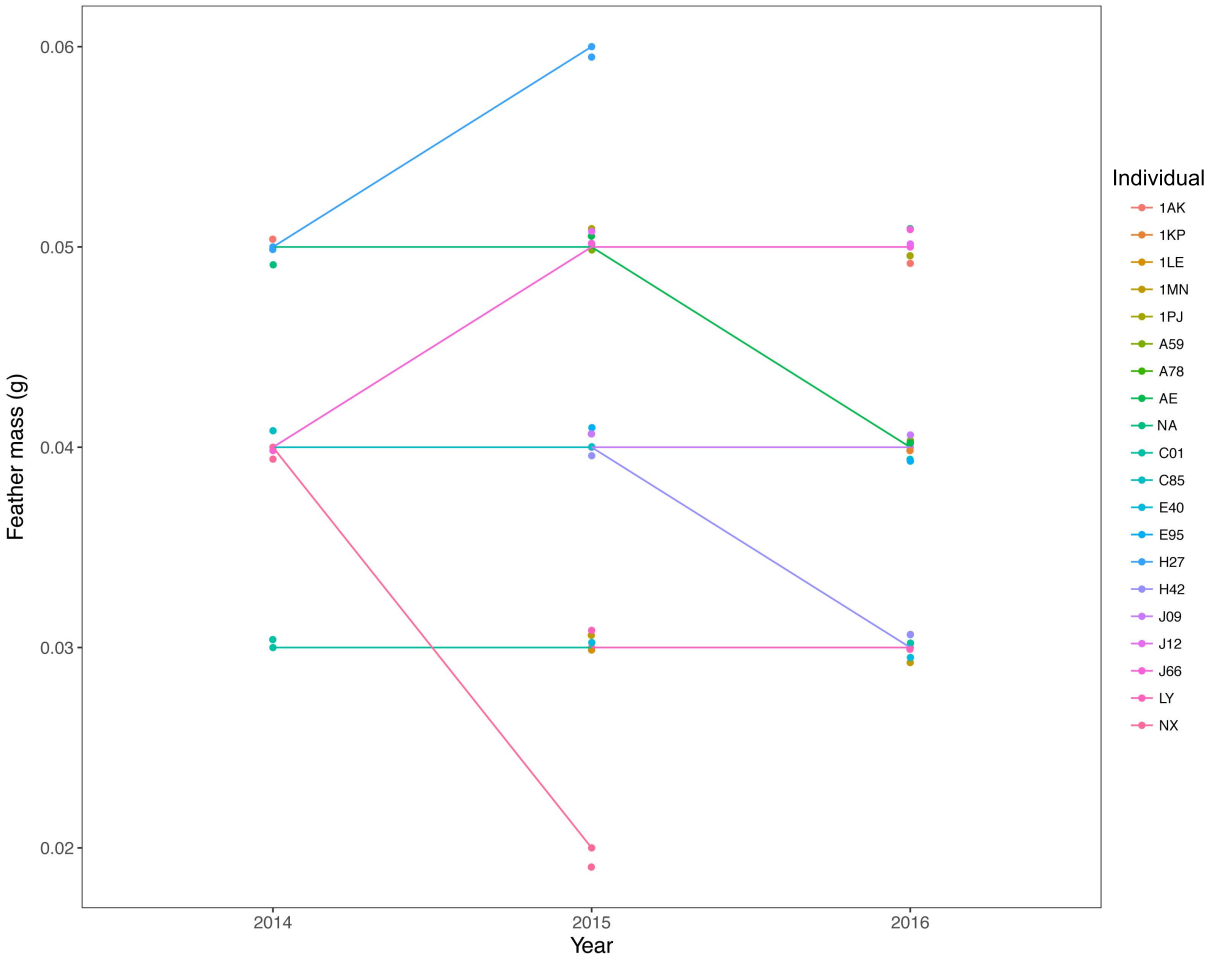

Figure G2. Feather mass did not vary among years for individual Hudsonian Godwits (*Limosa haemastica*) breeding at Beluga River, Alaska.

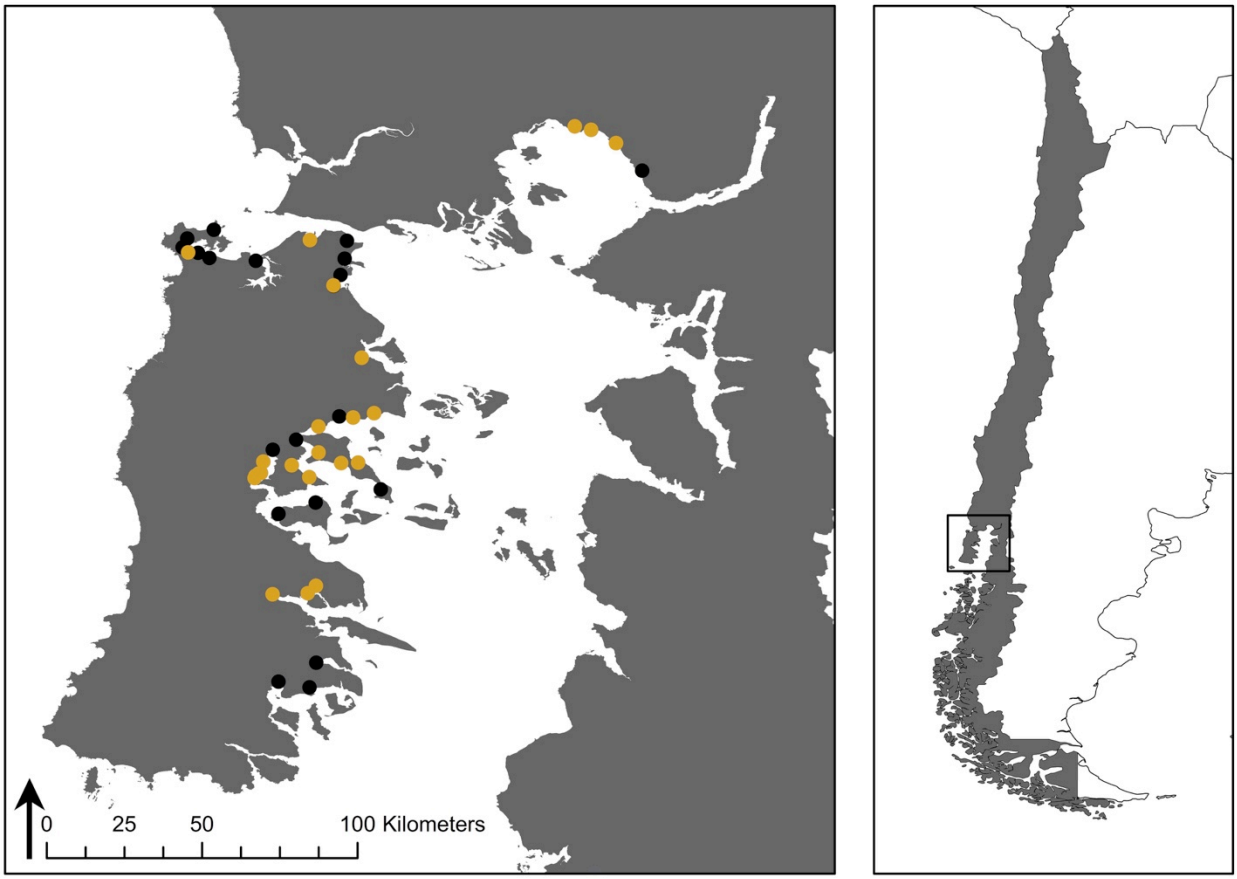

Figure G3. Survey sites (black) including locations (yellow) where marked Hudsonian Godwits (*Limosa haemastica*) from the Beluga River, Alaska, USA breeding population were found on the non-breeding grounds in 2015 and 2016 on or near Chiloé Island, Chile.

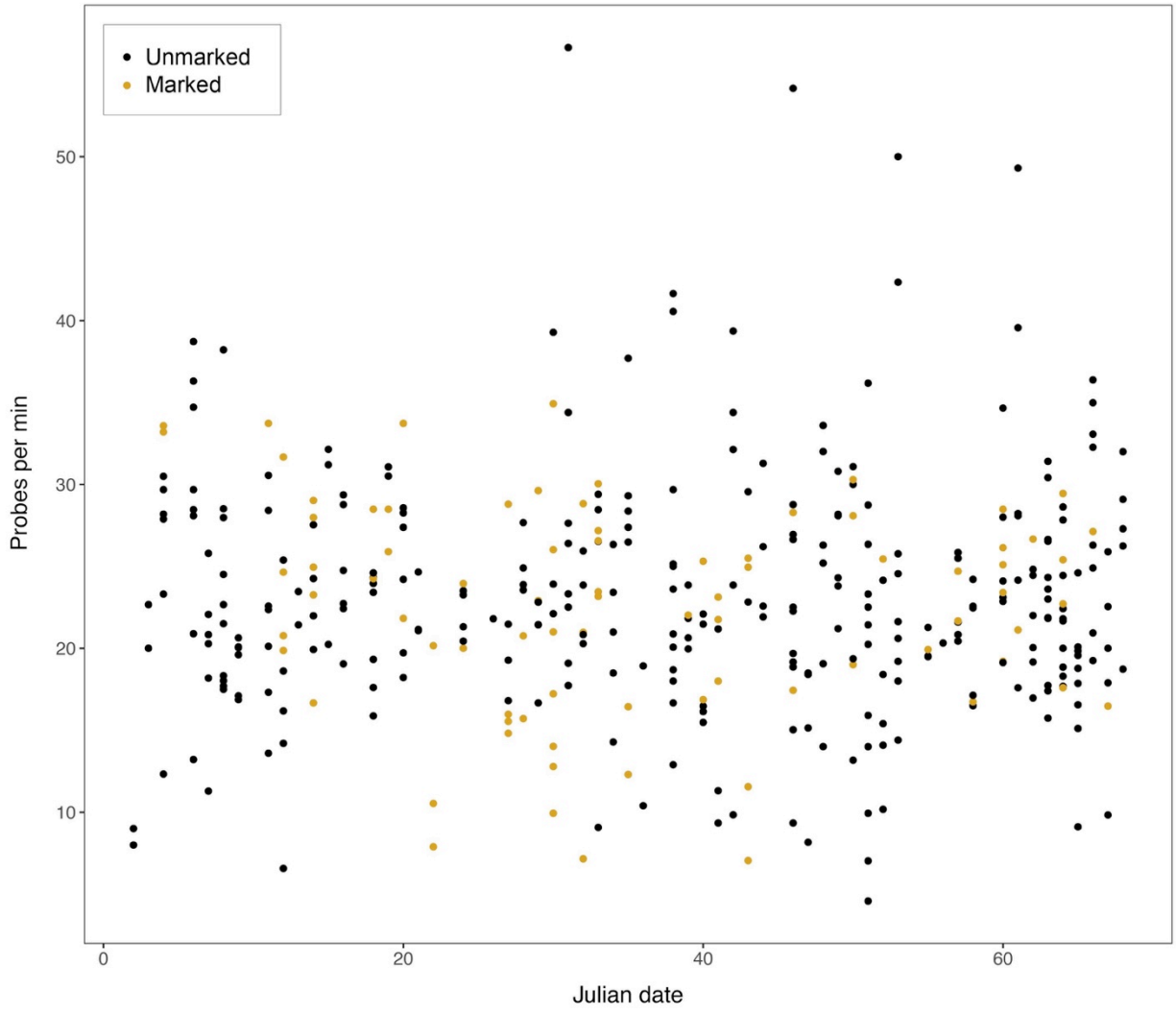

Figure G4. Probes per minute from focal foraging observations of Hudsonian Godwits (*Limosa haemastica*) throughout the non-breeding season (January to March). Individuals from the Beluga River, Alaska, USA population (yellow) are shown compared to unmarked individuals (black).

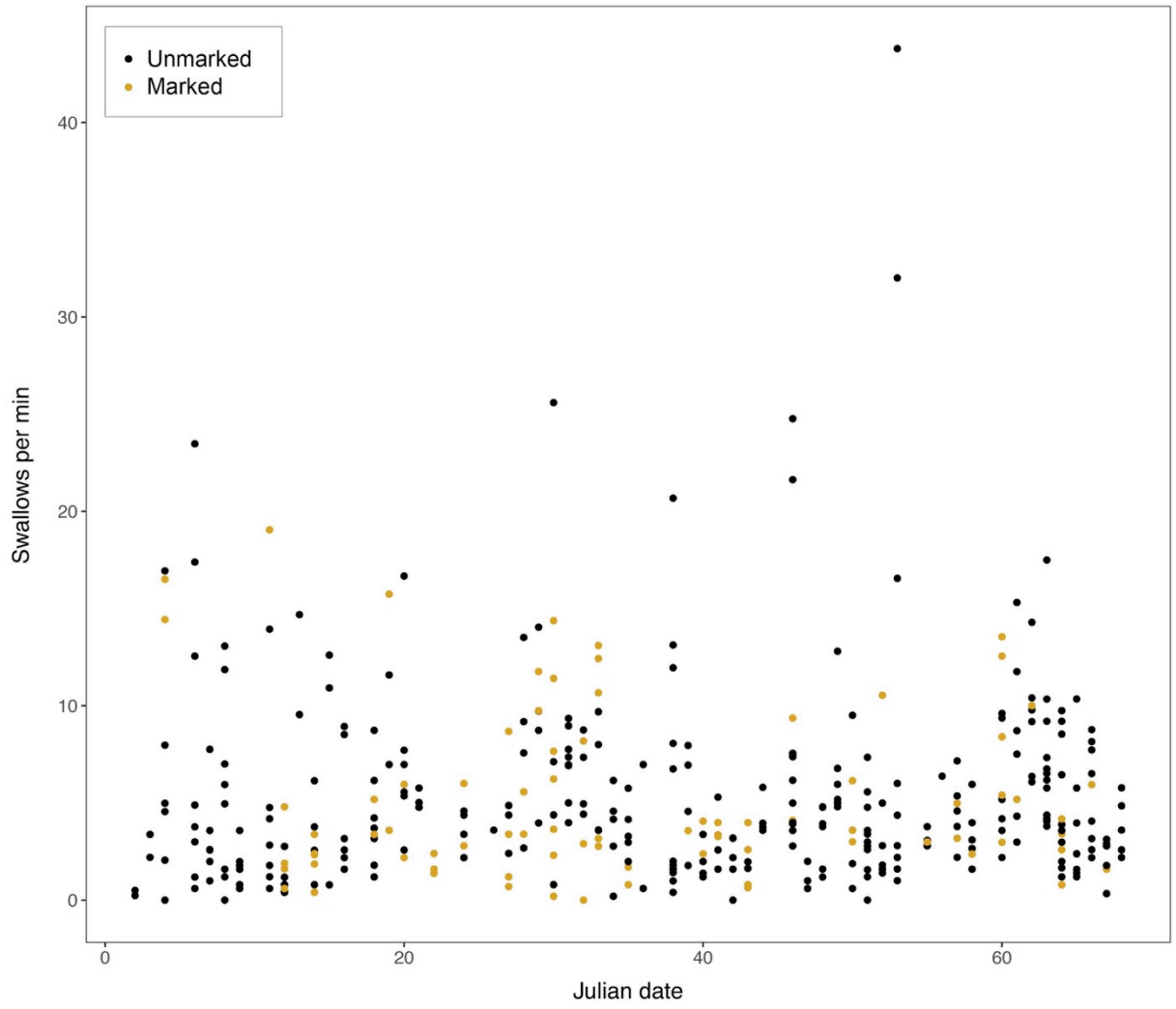

Figure G5. Swallows per minute from focal foraging observations of Hudsonian Godwits (*Limosa haemastica*) throughout the non-breeding season (January to March). Individuals from the Beluga River, Alaska, USA population (yellow) are shown compared to unmarked individuals (black).

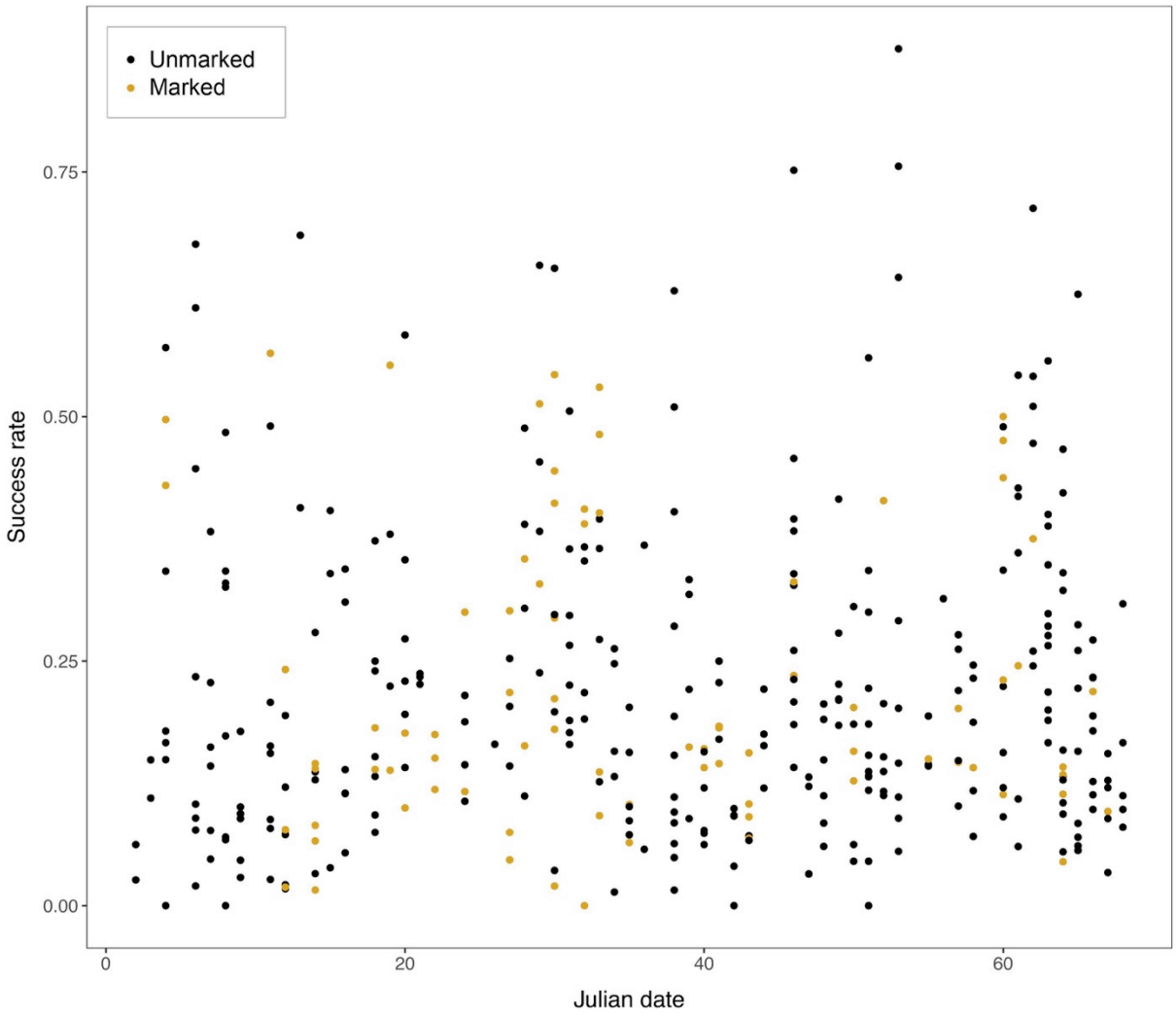

Figure G6. Success rate of individuals from focal foraging observations of Hudsonian Godwits (*Limosa haemastica*) throughout the non-breeding season (January to March). Individuals from the Beluga River, Alaska, USA population (yellow) are shown compared to unmarked individuals (black).

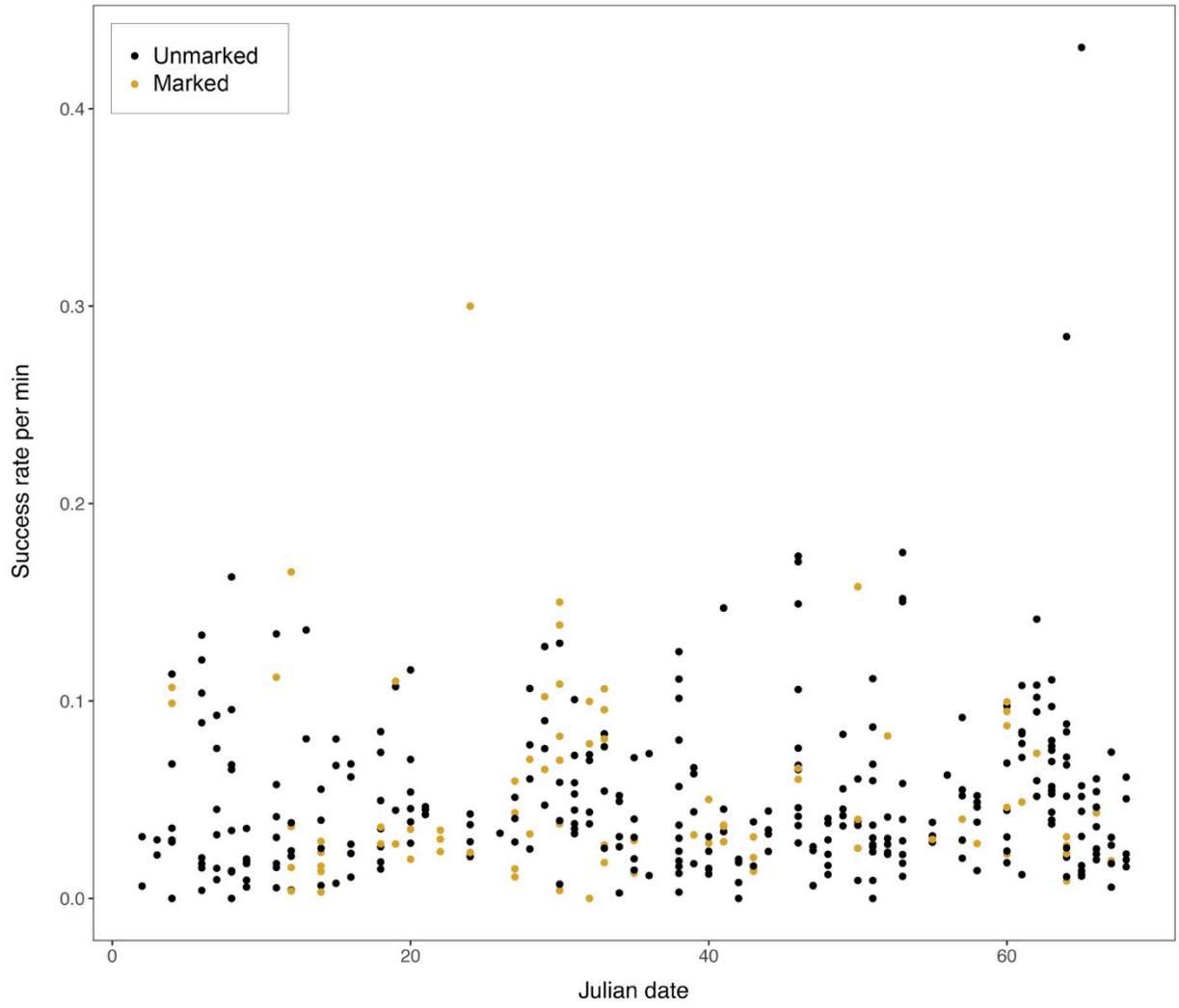

Figure G7. Success rate per minute from focal foraging observations of Hudsonian Godwits (*Limosa haemastica*) throughout the non-breeding season (January to March). Individuals from the Beluga River, Alaska, USA population (yellow) are shown compared to unmarked individuals (black).

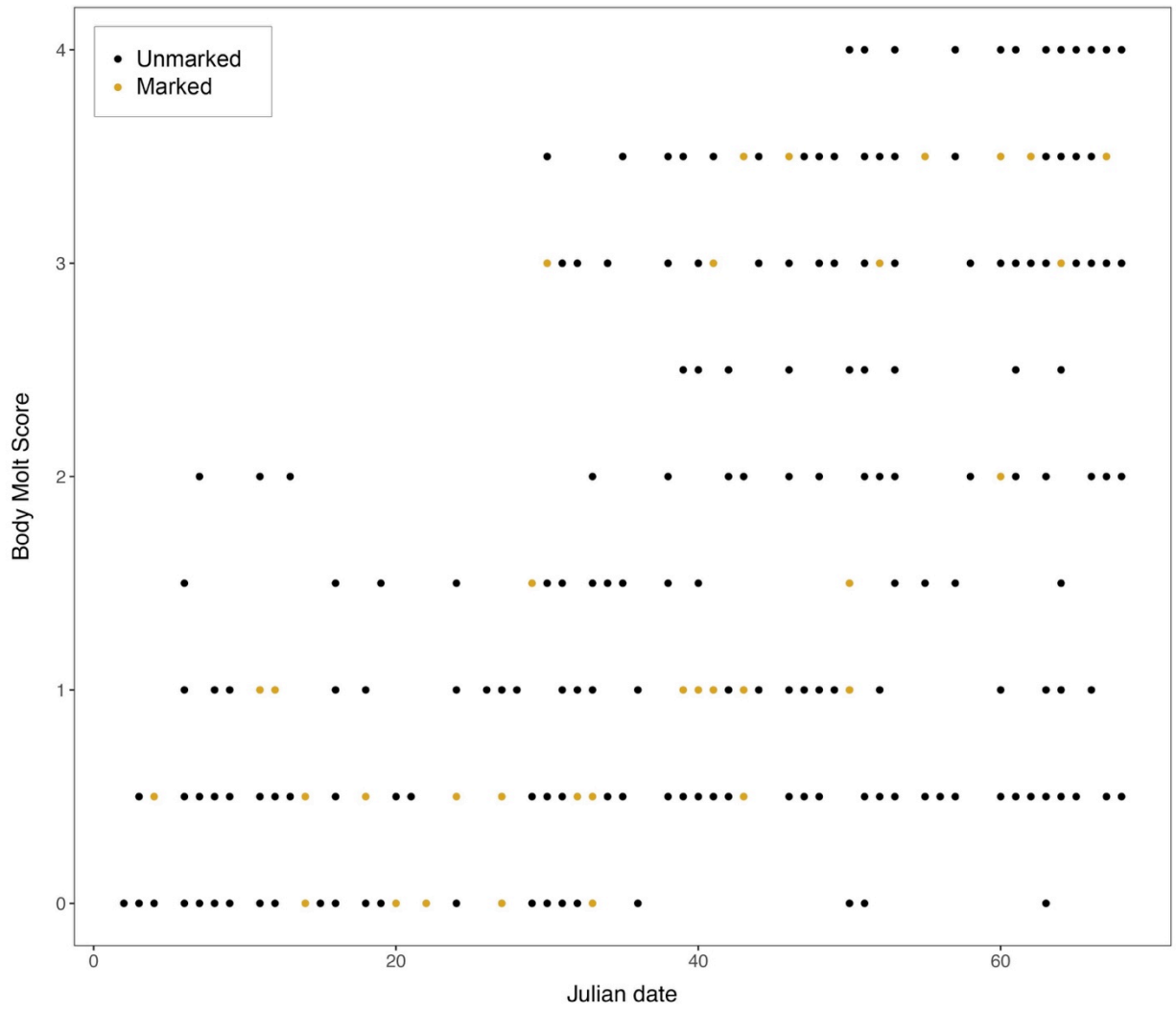

Figure G8. Body molt scores from focal foraging observations of Hudsonian Godwits (*Limosa haemastica*) throughout the non-breeding season (January to March). Individuals from the Beluga River, Alaska, USA population (yellow) are shown compared to unmarked individuals (black).

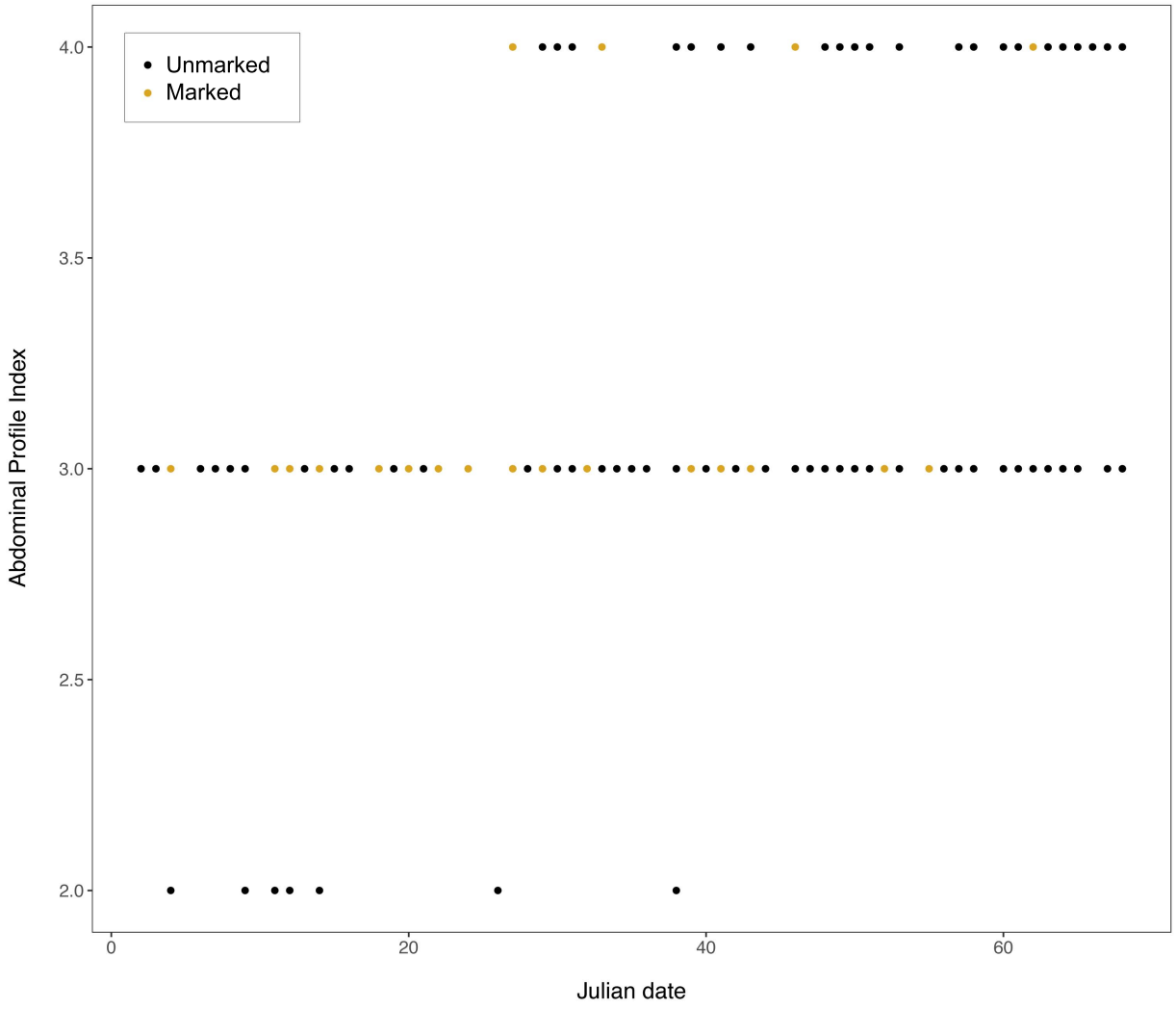

Figure G9. Abdominal profile index from focal foraging observations of Hudsonian Godwits (*Limosa haemastica*) throughout the non-breeding season (January to March). Individuals from the Beluga River, Alaska, USA population (yellow) are shown compared to unmarked individuals (black).

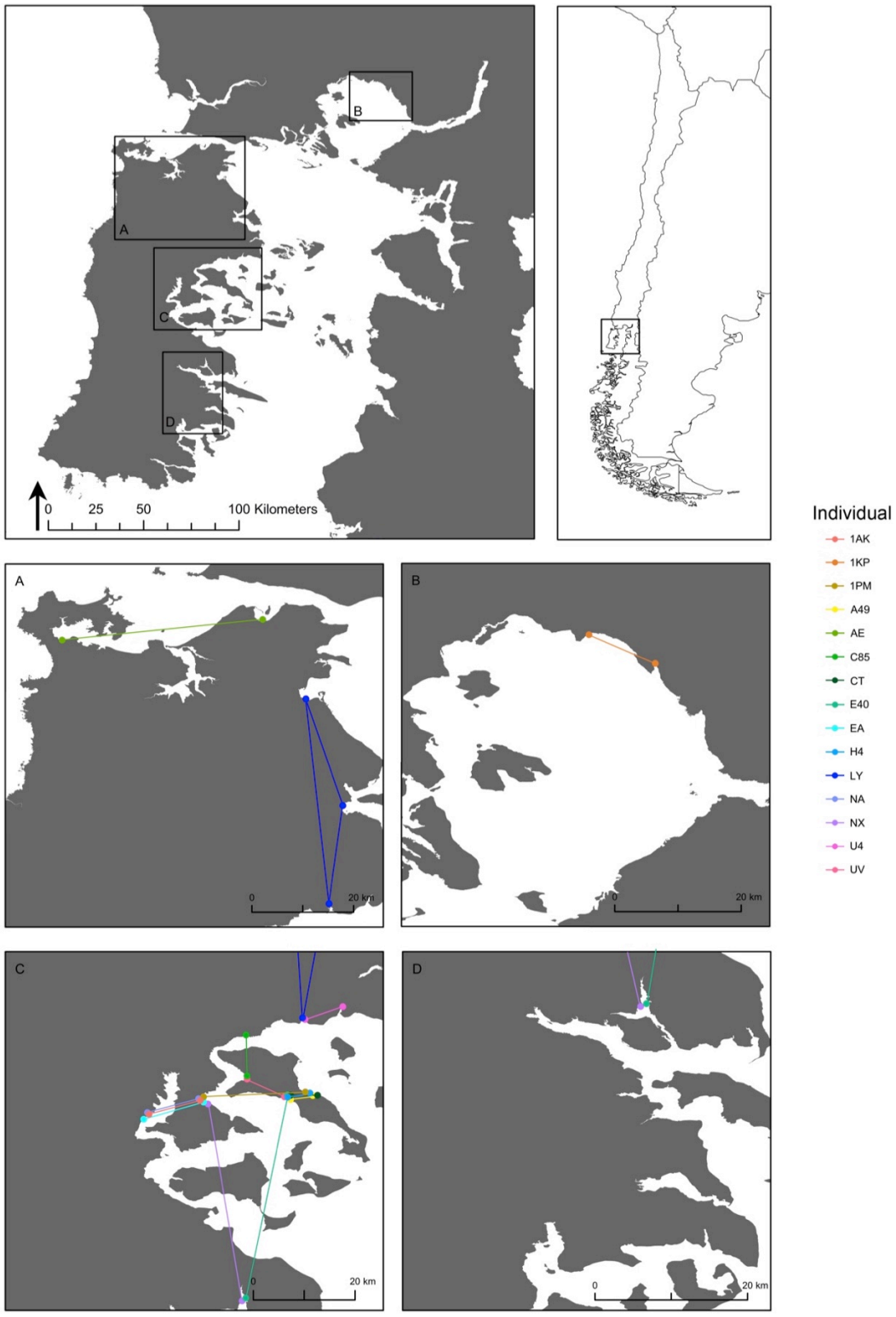

Figure G10. Movements of individual Hudsonian Godwits (*Limosa haemastica*) from our marked breeding population at Beluga River, Alaska, USA among intertidal mudflats on or near Chiloé Island in 2016.

APPENDIX H

Table HI. Non-breeding season data for linked observations of individual Hudsonian Godwits (*Limosa haemastica*) from the non-breeding grounds in southern Chile in 2015 and 2016.

Flag	Patch Quality		Body Condition			Foraging Success			
	Flock Density	Flock Condition	Condition residuals	BMS	API	Probes per min	Success Rate	Swallows per min	Success Rate per min
1AK	0.58	0.63	1.94	1.0	1.0	15.54	4.34	3.39	0.04
1KP	1.96	0.70	2.03	2.0	0.0	12.76	2.94	1.19	0.04
1LE	0.19	0.90	2.12	0.0	0.0	17.44	6.03	4.10	0.06
1MP	-0.67	-0.79	0.63	0.0	0.0	15.35	2.69	2.00	0.03
1PE	NA	NA	0.67	0.0	-0.3	30.85	2.65	2.35	0.02
1PE	1.23	0.82	1.37	0.2	0.1	24.13	5.14	5.60	0.05
1PM	0.37	0.75	1.68	0.0	-0.4	24.54	2.69	3.32	0.03
A49	1.47	0.56	2.53	2.0	1.0	22.49	6.81	8.86	0.07
AE	1.80	0.52	2.81	0.3	0.5	22.14	7.75	6.79	0.08
NA	0.54	0.78	1.38	0.0	0.0	20.14	3.02	3.44	0.03
C01	1.48	0.69	0.01	0.0	0.0	24.64	3.65	1.90	0.04
C85	2.15	0.86	2.83	0.7	1.0	25.20	8.23	10.54	0.08
CJ	-0.28	0.59	0.36	0.0	-1.0	27.13	2.34	2.94	0.02
CK	-0.67	-0.79	-0.05	-1.0	0.0	33.73	1.20	1.05	0.01
CT	0.77	0.73	0.25	-1.5	-0.3	24.36	3.23	3.46	0.03
E40	2.32	0.81	1.47	-0.5	0.5	20.69	3.18	3.66	0.03
E95	3.28	1.59	2.60	0.5	0.8	27.19	6.13	7.96	0.06
EA	NA	NA	1.56	0.2	0.0	22.89	4.58	4.91	0.05
EA	0.81	0.83	1.37	1.0	0.2	16.88	5.24	5.70	0.06
H4	1.72	0.68	1.91	1.0	0.5	15.01	5.39	2.98	0.06
J12	1.30	0.70	1.36	0.4	0.0	27.71	4.61	5.90	0.05
LY	0.15	0.61	1.42	1.0	0.0	23.09	2.94	3.46	0.03
NX	0.16	0.88	2.46	0.5	1.0	24.98	4.76	6.27	0.05
UV	NA	NA	1.37	0.2	0.2	28.75	5.12	5.50	0.05
UV	2.29	0.55	0.79	0.0	0.0	21.75	6.03	3.82	0.06

Table HII. Breeding performance data for linked observations of individual Hudsonian Godwits (*Limosa haemastica*) from the breeding grounds at Beluga River, Alaska in 2015 and 2016.

Flag	Breeding Performance					
	Return	Nest Initiation Date	Nest Fate	Chick Fate	Number of Days Brood Survived	Last Day Defending
1AK	Yes	128	Hatch	Survived	17	158
1KP	Yes	132	Hatch	Died	14	176
1LE	Yes	135	Hatch	Died	4	169
1MP	No	NA	NA	NA	NA	NA
1PE	No	NA	NA	NA	NA	NA
1PE	Yes	131	Hatch	Died	13	167
1PM	Yes	130	Hatch	Survived	20	172
A49	Yes	128	Fail	Died	0	NA
AE	Yes	128	Hatch	Died	3	156
NA	Yes	144	Hatch	Died	3	169
C01	Yes	128	Hatch	Survived	17	158
C85	Yes	130	Hatch	Survived	20	173
CJ	No	NA	NA	NA	NA	NA
CK	No	NA	NA	NA	NA	NA
CT	No	NA	NA	NA	NA	NA
E40	Yes	131	Hatch	Survived	16	184
E95	Yes	132	Hatch	Died	14	179
EA	Yes	NA	Fail	Died	0	NA
EA	Yes	129	Hatch	Died	2	157
H4	Yes	144	Hatch	Died	3	167
J12	Yes	131	Hatch	Died	12	166
LY	Yes	128	Hatch	Died	3	156
NX	Yes	NA	Fail	Died	0	NA
UV	Yes	NA	Hatch	Died	NA	NA
UV	Yes	129	Fail	Died	0	NA

Table HIII. Data for Hudsonian Godwit (*Limosa haemastica*) feather growth bar width, mass, and length and linked reproductive performance measures from 2014 to 2016 in Beluga River, Alaska, USA.

Flag	Sex	Year	Average growth bar width	Mass (g)	Length (mm)	Nest Fate	Chick Fate	Nest Initiation Date	Number of days brood survived	Last day defending
1AK	F	2014	55.05	0.05	89.35	Hatch	Survived	133	30	188
C01	M	2014	48.60	0.03	81.55	Hatch	Survived	133	30	181
C51	M	2014	50.45	0.03	82.00	Hatch	Survived	131	35	186
C85	M	2014	58.55	0.04	87.25	Hatch	Died	137	19	163
CK	M	2014	53.60	0.03	84.95	Hatch	Died	132	12	162
H18	M	2014	54.25	0.03	85.70	Hatch	Died	133	19	177
H27	F	2014	56.90	0.05	91.95	Hatch	Survived	141	23	189
H70	F	2014	49.90	0.05	91.60	Hatch	Survived	131	35	182
J88	F	2014	56.80	0.05	87.90	Hatch	Died	136	19	177
NA	F	2014	49.75	0.05	84.50	Hatch	Died	129	12	167
NX	M	2014	51.87	0.04	82.05	Hatch	Died	145	7	177
1KP	F	2015	53.10	0.04	89.95	Hatch	Survived	128	24	178
1LE	M	2015	51.60	0.03	84.75	Hatch	Died	138	11	174
1MN	M	2015	58.60	0.03	82.70	Hatch	Survived	129	20	176
1PE	M	2015	51.50	0.04	87.25	Hatch	Died	131	13	167
1PH	M	2015	54.10	0.03	86.45	Hatch	Died	129	7	162
1PJ	F	2015	48.70	0.05	88.70	Hatch	Died	128	4	158
A01	F	2015	56.60	0.05	92.15	Hatch	Died	132	19	177
A49	M	2015	52.70	0.03	85.35	Hatch	Died	138	14	177
A59	F	2015	55.00	0.05	87.95	Hatch	Died	138	11	179
A92	M	2015	56.40	0.03	83.25	Hatch	Died	130	21	177
AE	F	2015	60.90	0.05	88.60	Hatch	Died	128	21	175
AY	F	2015	52.80	0.06	92.10	Hatch	Died	129	2	157
C85	M	2015	57.95	0.04	86.90	Hatch	Died	128	9	163
CX	M	2015	52.55	0.03	85.50	Hatch	Died	128	9	163
E00	F	2015	57.20	0.05	92.80	Hatch	Died	130	5	161
E40	M	2015	50.70	0.03	84.40	Hatch	Survived	131	21	179
E95	M	2015	60.90	0.04	84.75	Hatch	Survived	128	26	180
EA	M	2015	53.85	0.03	88.00	Hatch	Died	129	2	157
H27	F	2015	57.00	0.06	91.45	Hatch	Died	138	19	182
H42	M	2015	57.60	0.04	85.20	Hatch	Died	132	19	177
J09	F	2015	49.70	0.04	83.80	Hatch	Died	134	10	171
J12	F	2015	57.65	0.05	90.60	Hatch	Survived	129	20	176
J25	F	2015	56.30	0.05	89.35	Hatch	Died	129	11	166
J66	F	2015	56.55	0.05	89.00	Hatch	Died	128	7	161

TABLE HIII (CONTINUED)

Flag	Sex	Year	Average growth bar width	Mass (g)	Length (mm)	Nest Fate	Chick Fate	Nest Initiation Date	Number of days brood survived	Last day defending
LY	M	2015	53.35	0.03	83.45	Hatch	Died	128	21	175
NX	M	2015	54.45	0.02	81.60	Hatch	Died	134	13	174
VY	F	2015	55.60	0.06	92.95	Hatch	Died	131	13	167
1AK	F	2016	53.90	0.05	89.10	Hatch	Survived	128	17	158
1EK	M	2016	61.20	0.03	81.95	Hatch	Died	136	5	166
1KL	F	2016	59.80	0.04	86.35	Hatch	Died	133	10	168
1KP	F	2016	54.45	0.04	89.50	Hatch	Died	132	14	176
1LE	M	2016	49.50	0.03	84.35	Hatch	Died	135	4	169
1MN	M	2016	54.70	0.03	82.35	Hatch	Died	131	12	166
1PJ	F	2016	59.95	0.05	88.20	Fail	Died	128	NA	NA
1PM	F	2016	48.85	0.05	85.85	Hatch	Survived	130	20	172
1TH	M	2016	60.65	0.04	82.30	Hatch	Died	133	13	171
A59	F	2016	60.75	0.04	88.00	Hatch	Died	135	4	169
A78	F	2016	59.10	0.04	87.35	Hatch	Survived	131	16	184
AE	F	2016	56.10	0.04	89.80	Hatch	Died	128	3	156
C01	M	2016	60.50	0.03	82.75	Hatch	Survived	128	17	158
C85	M	2016	59.10	0.04	88.20	Hatch	Survived	130	20	173
E40	M	2016	60.70	0.03	84.90	Hatch	Survived	131	16	184
E95	M	2016	56.90	0.04	84.20	Hatch	Died	132	14	179
H4	M	2016	59.05	0.04	87.65	Hatch	Died	144	3	167
H42	M	2016	56.60	0.03	84.20	Fail	Died	137	NA	NA
J09	F	2016	49.85	0.04	82.30	Hatch	Died	136	5	166
J12	F	2016	57.95	0.05	90.75	Hatch	Died	131	12	166
J66	F	2016	54.25	0.05	88.75	Fail	Died	137	NA	NA
LY	M	2016	52.70	0.03	81.75	Hatch	Died	128	3	156
M6	M	2016	56.25	0.03	85.10	Fail	Died	137	NA	NA
NA	F	2016	54.80	0.05	87.63	Hatch	Died	144	3	169

Table HIV. Encounter histories of Hudsonian Godwit (*Limosa haemastica*) annual survival from the non-breeding grounds in Chiloé Island, Chile. Each non-breeding season spans from October to March (e.g., 2006 – 2007; October 2006 – March 2007). A "1" denotes the individuals was seen or captured during that non-breeding season, and a "0" specifies the individual was either not seen or had not yet been marked.

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
00	1	1	0	1	0	0	Yes	No
01	0	1	0	1	1	1	No	Yes
04	1	0	0	0	1	1	No	Yes
06	1	0	0	0	0	0	Yes	No
07	1	0	0	0	0	0	Yes	No
08	1	1	0	1	1	0	Yes	No
10	1	1	0	0	1	0	No	No
25	0	0	0	0	1	1	No	No
50	0	1	0	1	0	0	No	Yes
51	0	1	0	1	0	1	Yes	No
52	0	1	0	1	1	1	No	Yes
53	0	1	1	0	0	0	No	Yes
54	0	1	0	0	0	0	Yes	No
55	0	1	1	0	0	0	No	Yes
56	0	1	0	0	0	0	No	Yes
57	0	1	0	0	1	0	Yes	No
58	0	1	0	1	1	1	Yes	No
59	0	1	0	0	0	0	No	Yes
60	0	1	0	0	1	0	Yes	No
61	0	1	1	1	1	1	No	Yes
62	0	1	0	0	1	1	No	Yes
63	0	1	0	0	0	0	No	Yes
64	0	1	1	0	0	0	Yes	No
65	0	1	0	0	0	0	No	No
66	0	1	0	0	0	0	No	Yes
67	0	1	0	1	1	1	No	Yes
68	0	1	0	1	1	0	Yes	No
69	0	1	1	0	1	1	No	Yes
70	0	1	0	0	0	0	No	Yes
71	0	1	0	1	1	1	No	Yes
72	0	1	1	1	0	0	Yes	No
73	0	1	0	0	0	1	Yes	No
74	0	1	0	0	0	1	No	Yes
75	0	1	1	0	0	0	Yes	No
76	0	1	1	0	0	1	Yes	No
77	0	1	0	0	0	0	No	Yes
78	0	1	0	0	1	1	Yes	No
79	0	1	0	0	0	0	No	No
80	0	1	0	0	0	0	No	Yes
81	0	1	0	1	1	0	Yes	No
82	0	1	1	1	1	1	No	Yes
83	0	1	0	0	1	0	No	Yes
84	0	1	0	0	0	0	Yes	No
85	0	1	0	0	1	1	No	Yes
86	0	1	0	0	0	0	No	Yes
87	0	1	1	1	1	0	No	No
88	0	1	0	1	1	1	No	Yes
89	0	1	0	0	0	0	No	Yes
90	0	1	0	1	1	1	Yes	No
91	0	1	0	1	1	0	No	Yes
92	0	1	1	1	1	0	Yes	No
93	0	1	0	0	0	0	No	Yes
94	0	1	0	0	0	0	Yes	No
95	0	1	1	0	0	1	No	Yes

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
96	0	1	0	0	0	0	Yes	No
97	0	1	0	0	0	0	No	Yes
98	0	1	0	0	0	0	No	No
99	0	1	0	0	0	0	No	Yes
A0	0	1	0	0	0	0	No	Yes
A1	0	1	0	0	0	0	No	Yes
A2	0	1	0	0	1	0	No	Yes
A3	0	1	1	1	1	1	Yes	No
A4	0	1	1	1	1	1	No	Yes
A5	0	1	1	1	1	1	No	Yes
A6	0	1	0	0	0	0	No	Yes
A7	0	1	1	1	1	0	Yes	No
A8	0	1	0	0	0	1	No	Yes
A9	0	1	0	0	0	0	Yes	No
AAA	0	0	1	0	0	0	Yes	No
AAC	0	0	1	1	0	1	No	Yes
AAE	0	0	1	0	0	1	No	No
AAH	0	0	1	0	1	1	Yes	No
AAJ	0	0	1	0	0	0	No	Yes
AAK	0	0	1	0	0	0	No	Yes
AAL	0	0	1	1	1	1	No	Yes
AAM	0	0	1	0	0	0	No	No
AAN	0	0	1	0	1	1	No	Yes
AAP	0	0	1	1	1	0	No	Yes
AAT	0	0	1	0	0	0	No	No
AAU	0	0	1	1	1	1	No	Yes
AAX	0	0	1	0	0	0	No	Yes
AAY	0	0	1	0	1	1	No	No
ACA	0	0	1	1	1	1	No	No
ACC	0	0	1	1	1	1	No	No
ACE	0	0	1	0	0	0	No	No
ACH	0	0	1	1	1	0	Yes	No
ACJ	0	0	1	1	0	0	Yes	No
ACK	0	0	1	0	1	1	Yes	No
ACL	0	0	1	0	1	0	Yes	No
ACM	0	0	1	1	0	0	No	No
ACP	0	0	1	0	1	1	Yes	No
ACT	0	0	1	1	1	0	No	Yes
ACU	0	0	1	0	0	1	No	No
ACV	0	0	1	0	1	1	No	No
ACX	0	0	1	0	1	0	Yes	No
ACY	0	0	1	0	1	0	Yes	No
AEA	0	0	1	1	0	0	No	Yes
AEC	0	0	1	0	0	1	Yes	No
AEE	0	0	1	0	0	0	No	No
AEH	0	0	1	1	1	1	No	Yes
AEJ	0	0	1	0	1	1	No	No
AEK	0	0	1	1	1	1	No	Yes
AEL	0	0	1	0	0	0	No	Yes
AEM	0	0	1	0	0	0	Yes	No
AEN	0	0	1	1	0	0	No	Yes
AEP	0	0	1	1	1	1	Yes	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
AET	0	0	1	0	0	0	No	No
AEU	0	0	1	1	1	1	No	Yes
AEV	0	0	1	0	1	1	No	No
AEX	0	0	1	0	1	0	No	No
AEY	0	0	1	1	1	1	No	No
AHA	0	0	1	0	0	0	No	Yes
AHC	0	0	1	1	0	0	Yes	No
AHE	0	0	1	0	0	0	Yes	No
AHH	0	0	1	1	0	0	No	No
AHJ	0	0	1	0	1	0	No	No
AHK	0	0	1	0	0	0	Yes	No
AHL	0	0	1	0	1	1	Yes	No
AHM	0	0	1	1	0	0	Yes	No
AHN	0	0	1	0	0	0	No	No
AHP	0	0	1	1	1	1	Yes	No
AHT	0	0	1	0	1	1	Yes	No
AHU	0	0	1	0	1	1	Yes	No
AHV	0	0	1	0	1	0	No	Yes
AHX	0	0	1	0	1	0	No	Yes
AHY	0	0	1	1	0	0	No	Yes
AJA	0	0	1	1	1	1	No	No
AJC	0	0	1	1	1	1	Yes	No
AJE	0	0	1	0	0	0	No	No
AJH	0	0	1	1	1	0	No	Yes
AJJ	0	0	1	0	1	0	No	Yes
AJK	0	0	1	0	0	0	No	Yes
AJL	0	0	1	1	1	1	Yes	No
AJM	0	0	1	0	0	0	No	No
AJN	0	0	1	1	0	0	No	Yes
AJP	0	0	1	1	1	1	No	No
AJT	0	0	1	1	1	0	No	Yes
AJU	0	0	1	0	1	1	No	No
AJV	0	0	1	0	0	0	No	No
AJX	0	0	1	1	0	0	No	Yes
AJY	0	0	1	0	0	0	No	Yes
AKA	0	0	1	1	1	1	No	No
AKC	0	0	1	1	1	1	No	No
AKE	0	0	1	1	1	1	Yes	No
AKH	0	0	1	0	0	0	Yes	No
AKJ	0	0	1	0	0	1	Yes	No
AKK	0	0	0	1	1	0	No	No
AKL	0	0	0	1	1	1	Yes	No
AKM	0	0	0	1	1	1	Yes	No
AKN	0	0	0	1	1	1	No	No
AKP	0	0	0	1	0	0	Yes	No
AKT	0	0	0	1	1	1	No	Yes
AKU	0	0	0	1	1	1	No	Yes
AKV	0	0	0	1	1	0	No	Yes
AKX	0	0	0	1	1	1	No	Yes
AKY	0	0	0	1	1	0	No	Yes
ALA	0	0	1	1	1	1	No	Yes
ALE	0	0	1	0	0	0	Yes	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
ALH	0	0	1	1	1	1	Yes	No
ALJ	0	0	1	0	0	0	Yes	No
ALK	0	0	1	1	1	1	Yes	No
ALL	0	0	1	0	0	0	No	Yes
ALM	0	0	1	0	1	1	No	Yes
ALN	0	0	1	1	1	1	No	Yes
ALP	0	0	1	1	0	0	Yes	No
ALT	0	0	1	0	0	0	No	Yes
ALU	0	0	1	0	1	0	Yes	No
ALV	0	0	1	0	0	0	No	Yes
ALX	0	0	1	0	1	1	Yes	No
ALY	0	0	1	1	0	0	No	Yes
AMA	0	0	1	1	1	1	No	No
AMC	0	0	1	1	1	1	No	No
AME	0	0	1	1	1	1	No	Yes
AMH	0	0	1	1	1	1	No	No
AMJ	0	0	1	0	0	0	Yes	No
AMK	0	0	1	1	0	1	Yes	No
AML	0	0	1	1	1	1	Yes	No
AMM	0	0	1	1	1	1	Yes	No
AMN	0	0	1	0	1	1	No	Yes
AMP	0	0	1	0	1	1	Yes	No
AMT	0	0	1	1	1	1	Yes	No
AMU	0	0	1	1	1	0	No	Yes
AMV	0	0	1	1	1	1	Yes	No
AMX	0	0	1	0	0	0	No	Yes
AMY	0	0	1	1	1	0	No	No
ANA	0	0	1	1	0	0	No	No
ANC	0	0	1	1	1	1	Yes	No
ANE	0	0	1	0	0	1	No	Yes
ANH	0	0	1	0	0	0	No	Yes
ANJ	0	0	1	1	0	0	No	Yes
ANK	0	0	1	1	1	1	Yes	No
ANL	0	0	1	1	1	0	No	Yes
ANM	0	0	1	0	1	0	No	No
ANN	0	0	1	1	1	0	No	Yes
ANP	0	0	1	1	1	1	Yes	No
ANT	0	0	1	0	0	0	Yes	No
ANU	0	0	1	0	1	1	Yes	No
ANV	0	0	1	1	1	1	Yes	No
ANX	0	0	1	0	0	0	Yes	No
ANY	0	0	1	1	1	1	No	No
APA	0	0	1	1	1	0	No	No
APC	0	0	1	1	1	1	Yes	No
APE	0	0	0	1	0	1	No	Yes
APH	0	0	0	1	0	1	Yes	No
APJ	0	0	0	1	0	1	No	Yes
APK	0	0	0	1	1	0	No	Yes
APL	0	0	0	1	0	0	No	Yes
APM	0	0	0	1	0	1	No	Yes
APN	0	0	0	1	1	1	No	Yes
APP	0	0	0	1	0	0	No	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
APT	0	0	0	1	1	1	No	No
APU	0	0	0	1	1	0	No	Yes
APV	0	0	0	1	1	1	No	Yes
APX	0	0	0	1	0	0	No	Yes
APY	0	0	0	1	1	1	No	Yes
ATA	0	0	0	1	1	0	No	No
ATC	0	0	0	1	0	0	No	Yes
ATE	0	0	0	1	1	0	No	Yes
ATH	0	0	0	1	1	1	No	Yes
ATJ	0	0	0	1	1	1	No	Yes
ATK	0	0	0	1	0	1	Yes	No
ATL	0	0	0	1	1	1	No	Yes
ATM	0	0	0	1	1	1	No	Yes
ATN	0	0	0	1	1	1	No	Yes
ATP	0	0	0	1	1	1	No	No
ATT	0	0	0	1	1	1	No	No
ATU	0	0	0	1	1	0	Yes	No
ATV	0	0	0	1	1	1	No	No
ATX	0	0	0	1	1	1	Yes	No
ATY	0	0	0	1	1	1	No	Yes
AUA	0	0	0	1	0	0	No	Yes
AUC	0	0	0	1	0	0	No	Yes
AUE	0	0	0	1	0	0	Yes	No
AUH	0	0	0	1	0	0	No	Yes
AUJ	0	0	0	1	0	0	No	Yes
AUK	0	0	0	1	1	0	No	No
AUL	0	0	0	1	0	1	No	Yes
AUM	0	0	0	1	0	1	No	Yes
AUN	0	0	0	1	0	1	Yes	No
AUP	0	0	0	1	0	1	No	Yes
AUT	0	0	0	1	1	1	Yes	No
AUU	0	0	0	1	1	0	No	Yes
AUV	0	0	0	1	1	1	No	Yes
AUX	0	0	0	1	1	0	No	No
AUY	0	0	0	1	0	1	No	Yes
AVA	0	0	0	1	0	0	No	Yes
AVC	0	0	0	1	0	0	Yes	No
AVE	0	0	0	1	0	1	No	Yes
AVH	0	0	0	1	0	0	No	Yes
AVJ	0	0	0	1	0	1	Yes	No
AVK	0	0	0	1	1	1	No	Yes
AVL	0	0	0	1	1	1	No	Yes
AVM	0	0	0	1	0	1	Yes	No
AVN	0	0	0	1	0	0	No	Yes
AVP	0	0	0	1	0	0	No	Yes
AVT	0	0	0	1	0	0	No	Yes
AVU	0	0	0	1	1	0	No	Yes
AVV	0	0	0	1	0	0	No	Yes
AVX	0	0	0	1	0	0	Yes	No
AVY	0	0	0	1	0	0	Yes	No
AX	0	0	0	1	1	1	No	No
AXA	0	0	0	1	0	0	Yes	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
AXC	0	0	0	1	0	0	No	Yes
AXE	0	0	0	1	1	0	No	Yes
AXH	0	0	0	1	1	0	No	Yes
AXJ	0	0	0	1	0	0	No	Yes
AXK	0	0	0	1	0	0	No	Yes
AXL	0	0	0	1	1	1	No	Yes
AXM	0	0	0	1	0	0	No	No
AXN	0	0	0	1	0	0	No	Yes
AXP	0	0	0	1	0	1	No	Yes
AXT	0	0	0	1	0	1	No	Yes
AXU	0	0	0	1	0	0	No	Yes
AXV	0	0	0	1	0	1	No	Yes
AXX	0	0	0	1	1	1	Yes	No
AXY	0	0	0	1	1	1	Yes	No
AYA	0	0	0	1	1	0	No	No
AYC	0	0	0	1	1	1	No	Yes
AYE	0	0	0	1	1	1	No	Yes
AYH	0	0	0	1	1	0	Yes	No
AYJ	0	0	0	1	0	0	No	Yes
AYK	0	0	0	1	0	0	No	Yes
AYL	0	0	0	1	1	1	No	Yes
AYM	0	0	0	1	1	1	Yes	No
AYN	0	0	0	1	1	0	No	Yes
AYP	0	0	0	1	0	0	Yes	No
AYT	0	0	0	1	0	0	No	Yes
AYU	0	0	0	1	1	1	No	Yes
AYV	0	0	0	1	1	1	Yes	No
AYX	0	0	0	1	0	1	Yes	No
AYY	0	0	0	1	1	1	Yes	No
C0	0	1	0	0	0	1	Yes	No
C1	0	1	0	0	1	1	No	Yes
C2	0	1	0	1	1	1	Yes	No
C3	0	1	1	1	1	1	No	No
C4	0	1	1	0	0	0	No	Yes
C5	0	1	0	0	0	0	Yes	No
C6	0	1	0	0	0	1	No	Yes
C7	0	1	0	0	0	0	No	Yes
C8	0	1	0	0	0	1	Yes	No
C9	0	1	0	0	0	0	No	Yes
CA	0	0	0	0	1	1	Yes	No
CAA	0	0	0	1	1	1	No	Yes
CAC	0	0	0	1	1	0	No	Yes
CAE	0	0	0	0	1	1	No	Yes
CAH	0	0	0	1	0	0	No	No
CAJ	0	0	0	1	0	1	No	Yes
CAK	0	0	0	1	1	1	No	Yes
CAL	0	0	0	1	1	1	No	Yes
CAM	0	0	0	1	1	1	Yes	No
CAN	0	0	0	1	1	0	No	Yes
CAP	0	0	0	1	0	0	Yes	No
CAT	0	0	0	1	1	1	No	No
CAU	0	0	0	1	1	0	Yes	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
CAV	0	0	0	1	1	0	No	Yes
CAX	0	0	0	1	1	0	Yes	No
CAY	0	0	0	1	0	0	Yes	No
CC	1	1	0	0	0	0	Yes	No
CCA	0	0	0	1	1	1	No	Yes
CCC	0	0	0	1	1	1	Yes	No
CCE	0	0	0	1	1	0	No	Yes
CCH	0	0	0	1	1	0	Yes	No
CCJ	0	0	0	1	1	1	No	No
CCK	0	0	0	1	1	1	No	Yes
CCL	0	0	0	1	1	1	Yes	No
CCM	0	0	0	1	0	1	No	Yes
CCN	0	0	0	1	1	1	No	Yes
CCP	0	0	0	1	1	1	No	Yes
CCT	0	0	0	1	0	0	No	No
CCU	0	0	0	1	1	1	No	No
CCV	0	0	0	1	1	1	No	Yes
CCX	0	0	0	1	0	0	No	No
CCY	0	0	0	1	1	1	No	Yes
CE	1	0	1	0	0	0	No	Yes
CEA	0	0	0	0	1	0	Yes	No
CEC	0	0	0	0	1	1	No	No
CEE	0	0	0	0	1	0	No	Yes
CEH	0	0	0	0	1	1	No	No
CEJ	0	0	0	0	1	1	Yes	No
CEK	0	0	0	0	1	1	Yes	No
CEL	0	0	0	0	1	0	Yes	No
CEM	0	0	0	0	1	1	Yes	No
CEN	0	0	0	0	1	1	Yes	No
CEP	0	0	0	0	1	1	No	No
CET	0	0	0	0	1	1	No	Yes
CEU	0	0	0	0	1	1	No	Yes
CEV	0	0	0	0	1	1	No	Yes
CEX	0	0	0	0	1	0	Yes	No
CEY	0	0	0	0	1	1	Yes	No
CH	1	0	0	0	1	0	No	No
CHA	0	0	0	0	1	1	Yes	No
CHC	0	0	0	0	1	1	No	No
CHE	0	0	0	1	1	0	No	Yes
CHH	0	0	0	1	0	1	No	Yes
CHJ	0	0	0	1	1	1	No	Yes
CHK	0	0	0	1	1	0	Yes	No
CHL	0	0	0	1	0	1	No	Yes
CHM	0	0	0	1	0	1	No	Yes
CHN	0	0	0	1	0	0	No	Yes
CHP	0	0	0	1	1	1	No	Yes
CHT	0	0	0	1	0	0	Yes	No
CHU	0	0	0	1	1	1	No	Yes
CHV	0	0	0	1	1	0	No	Yes
CHX	0	0	0	1	0	0	No	Yes
CHY	0	0	0	1	1	1	No	Yes
CJ	1	0	0	1	1	1	No	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
CJA	0	0	0	0	1	0	No	Yes
CJC	0	0	0	0	1	1	No	No
CJE	0	0	0	0	1	1	No	Yes
CJH	0	0	0	0	1	0	No	Yes
CJJ	0	0	0	0	1	0	No	No
CJK	0	0	0	0	1	1	Yes	No
CJL	0	0	0	0	1	1	No	Yes
CJM	0	0	0	0	1	1	No	Yes
CJN	0	0	0	0	1	1	No	No
CJP	0	0	0	0	1	1	Yes	No
CJT	0	0	0	0	1	1	No	Yes
CJU	0	0	0	0	1	1	Yes	No
CJV	0	0	0	0	1	0	Yes	No
CJX	0	0	0	0	1	0	No	Yes
CJY	0	0	0	0	1	0	No	No
CK	1	0	0	0	0	0	No	No
CKA	0	0	0	0	1	1	No	No
CKC	0	0	0	0	1	1	Yes	No
CKE	0	0	0	0	1	1	Yes	No
CKH	0	0	0	0	1	1	No	Yes
CKJ	0	0	0	0	1	1	No	Yes
CKK	0	0	0	0	1	1	No	Yes
CKL	0	0	0	0	1	0	No	Yes
CKN	0	0	0	0	1	0	No	Yes
CKP	0	0	0	0	1	1	Yes	No
CKT	0	0	0	0	1	0	Yes	No
CKU	0	0	0	0	1	1	Yes	No
CKV	0	0	0	0	1	0	Yes	No
CKX	0	0	0	0	1	0	No	Yes
CKY	0	0	0	0	1	0	No	Yes
CL	1	0	0	0	0	0	No	No
CLA	0	0	0	0	1	0	Yes	No
CLC	0	0	0	0	1	1	No	Yes
CLE	0	0	0	0	1	1	No	No
CLH	0	0	0	0	1	0	No	Yes
CLJ	0	0	0	0	1	0	Yes	No
CLK	0	0	0	0	1	0	Yes	No
CLL	0	0	0	0	1	1	Yes	No
CLM	0	0	0	0	1	1	Yes	No
CLN	0	0	0	0	1	0	Yes	No
CLP	0	0	0	0	1	0	Yes	No
CLT	0	0	0	0	1	0	Yes	No
CLU	0	0	0	0	1	1	Yes	No
CLV	0	0	0	0	1	1	No	Yes
CLX	0	0	0	0	1	0	No	Yes
CLY	0	0	0	0	1	1	No	Yes
CM	1	1	0	1	1	1	No	No
CMA	0	0	0	0	1	0	No	Yes
CMC	0	0	0	0	1	1	Yes	No
CME	0	0	0	0	1	1	No	Yes
CMH	0	0	0	0	1	1	No	Yes
CMJ	0	0	0	0	1	0	No	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
CMK	0	0	0	0	1	1	No	Yes
CML	0	0	0	0	1	1	No	No
CMM	0	0	0	0	1	1	No	Yes
CMN	0	0	0	0	1	1	No	No
CMP	0	0	0	0	1	1	No	No
CMV	0	0	0	0	1	0	No	Yes
CMX	0	0	0	0	1	1	No	Yes
CMY	0	0	0	0	1	1	No	Yes
CN	1	0	0	0	0	1	No	Yes
CNE	0	0	0	0	1	0	No	Yes
CNH	0	0	0	0	1	0	No	Yes
CP	1	0	0	0	0	0	No	No
CPC	0	0	0	0	1	0	No	Yes
CPE	0	0	0	0	1	1	No	Yes
CPH	0	0	0	0	1	1	No	Yes
CPL	0	0	0	0	1	0	No	Yes
CPM	0	0	0	0	1	1	No	Yes
CPN	0	0	0	0	1	1	Yes	No
CPT	0	0	0	0	1	0	Yes	No
CPU	0	0	0	0	1	1	Yes	No
CPV	0	0	0	0	1	0	Yes	No
CPX	0	0	0	0	1	0	Yes	No
CPY	0	0	0	0	1	1	No	Yes
CT	1	0	0	0	1	0	No	Yes
CTA	0	0	0	0	1	1	Yes	No
CTE	0	0	0	0	1	1	No	Yes
CTH	0	0	0	0	1	0	No	Yes
CTJ	0	0	0	0	1	1	No	Yes
CTL	0	0	0	0	1	1	No	Yes
CTM	0	0	0	0	1	1	Yes	No
CTN	0	0	0	0	1	1	Yes	No
CTP	0	0	0	0	1	1	Yes	No
CTT	0	0	0	0	1	1	Yes	No
CTX	0	0	0	0	1	1	Yes	No
CTY	0	0	0	0	1	1	Yes	No
CU	1	0	0	1	1	0	No	Yes
CUA	0	0	0	0	1	0	No	Yes
CUC	0	0	0	0	1	1	Yes	No
CUE	0	0	0	0	1	0	Yes	No
CUJ	0	0	0	0	1	0	Yes	No
CUL	0	0	0	0	1	1	No	Yes
CUM	0	0	0	0	1	1	Yes	No
CUN	0	0	0	0	1	1	No	Yes
CUT	0	0	0	0	1	1	No	Yes
CUV	0	0	0	0	1	1	No	Yes
CV	1	0	0	0	1	1	Yes	No
CX	1	1	0	0	1	0	No	No
CY	1	1	0	0	0	1	Yes	No
E0	0	1	0	0	0	0	No	Yes
E1	0	1	0	1	0	0	Yes	No
E2	0	1	0	0	1	0	No	Yes
E3	0	1	1	0	0	0	No	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
E4	0	1	0	0	1	0	No	Yes
E5	0	1	0	0	0	0	Yes	No
E6	0	1	0	0	0	0	Yes	No
E7	0	1	0	0	0	0	No	Yes
E8	0	1	0	0	0	0	No	Yes
E9	0	1	0	1	1	0	No	No
EA	1	1	0	0	0	0	No	Yes
EC	1	0	0	0	0	0	No	No
EE	1	0	0	0	0	1	No	Yes
EH	1	1	1	1	1	1	Yes	No
EJ	1	1	0	0	0	0	No	Yes
EK	1	0	0	0	0	0	No	Yes
EL	1	1	0	1	1	1	No	Yes
EM	1	0	0	0	0	0	Yes	No
EN	1	0	0	0	0	0	No	No
EP	1	0	0	0	0	1	Yes	No
ET	1	0	0	1	0	0	Yes	No
EU	1	0	0	0	0	0	No	No
EV	1	0	0	0	0	1	Yes	No
EX	1	0	0	1	1	1	Yes	No
EY	1	0	0	0	0	0	No	No
H0	0	1	1	1	1	0	Yes	No
H1	0	1	0	0	1	0	Yes	No
H2	0	1	0	0	0	0	Yes	No
H3	0	1	0	0	0	0	Yes	No
H4	0	1	0	0	0	0	No	Yes
H5	0	1	0	0	0	0	No	Yes
H6	0	1	0	0	0	0	Yes	No
H7	0	1	0	0	0	0	No	Yes
H8	0	1	0	1	0	0	Yes	No
H9	0	1	0	1	1	1	Yes	No
HA	1	1	0	0	1	0	No	Yes
HC	1	1	0	0	0	0	No	No
HE	1	1	0	1	0	0	No	Yes
HH	1	0	0	0	1	0	Yes	No
HJ	1	0	0	0	0	0	Yes	No
HK	1	0	0	0	0	0	Yes	No
HL	1	1	0	1	1	0	Yes	No
HM	1	1	0	0	0	0	No	Yes
HN	1	1	0	0	1	0	Yes	No
HP	1	0	0	0	0	0	Yes	No
HT	1	0	0	0	0	0	Yes	No
HU	1	1	0	0	1	0	Yes	No
HV	1	1	0	0	0	0	Yes	No
HX	1	0	0	1	0	0	No	Yes
HY	1	1	0	1	0	0	No	No
J0	0	1	0	0	0	0	No	No
J1	0	1	0	0	0	0	Yes	No
J2	0	1	1	0	0	0	Yes	No
J3	0	1	1	0	1	1	No	Yes
J4	0	1	0	0	1	1	No	No
J5	0	1	0	0	0	0	No	Yes

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
J6	0	1	0	0	0	0	No	Yes
J7	0	1	0	0	0	0	No	No
J8	0	1	0	0	1	0	No	Yes
J9	0	1	0	0	0	0	Yes	No
JA	1	0	0	0	0	0	Yes	No
JC	1	1	0	0	0	0	Yes	No
JE	1	0	0	0	0	0	Yes	No
JH	1	0	1	0	0	0	No	No
JJ	1	0	0	1	1	1	No	No
JK	1	0	0	0	0	0	No	No
JL	1	1	0	0	0	0	No	No
JM	1	1	0	0	0	0	No	No
JP	1	0	0	1	1	1	Yes	No
JT	1	1	0	1	1	1	No	Yes
JU	1	1	0	1	0	0	No	Yes
JV	1	0	0	0	0	0	Yes	No
K0	0	1	1	0	1	0	No	Yes
K1	0	1	0	0	1	1	Yes	No
K2	0	1	0	0	0	0	No	No
K3	0	1	0	0	0	0	Yes	No
K4	0	1	0	0	0	0	Yes	No
K5	0	0	1	0	0	0	No	Yes
K6	0	1	0	1	1	0	No	Yes
K7	0	1	0	0	0	0	No	Yes
K8	0	1	0	0	1	1	No	Yes
K9	0	1	1	1	1	1	No	Yes
KA	1	1	0	0	0	0	Yes	No
KC	1	0	0	0	1	1	No	Yes
KE	1	0	0	0	0	0	Yes	No
KH	1	1	1	0	1	0	No	Yes
KJ	1	1	1	1	1	0	Yes	No
KK	1	0	0	0	0	0	No	No
KL	1	1	1	1	1	1	No	Yes
KN	1	0	0	1	0	0	No	Yes
KT	1	1	1	0	0	0	Yes	No
KU	1	0	0	0	0	0	No	Yes
KV	1	0	0	0	0	0	Yes	No
KX	1	0	0	0	0	0	Yes	No
KY	1	0	0	0	0	0	No	Yes
L0	0	1	0	0	1	1	Yes	No
L1	0	1	0	0	0	0	No	Yes
L2	0	1	0	0	0	0	Yes	No
L3	0	1	0	0	0	0	No	Yes
L4	0	1	0	0	1	0	Yes	No
L5	0	1	0	0	0	0	No	Yes
L6	0	1	0	0	0	0	Yes	No
L7	0	0	1	0	0	0	Yes	No
L8	0	0	1	0	0	0	No	Yes
L9	0	0	1	1	0	0	No	Yes
LA	1	0	0	0	0	0	Yes	No
LC	1	0	1	1	0	1	No	Yes
LE	1	1	0	0	0	0	Yes	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
LH	1	0	0	0	1	1	No	No
LJ	1	1	1	0	0	0	Yes	No
LK	1	1	0	0	0	0	Yes	No
LL	1	1	0	1	1	1	No	Yes
LM	1	1	0	0	0	0	No	No
LN	1	1	1	1	1	0	No	No
LP	1	1	0	0	1	0	No	No
LT	1	0	0	0	1	1	Yes	No
LU	1	1	0	0	1	1	Yes	No
LV	1	1	1	1	1	1	Yes	No
LX	1	0	0	0	0	1	Yes	No
M0	0	0	1	0	1	1	No	Yes
M1	0	0	1	1	1	0	No	No
M2	0	0	1	1	0	1	No	Yes
M3	0	0	1	0	1	1	Yes	No
M4	0	0	1	1	1	1	No	Yes
M5	0	0	1	0	1	0	No	Yes
M6	0	0	1	1	0	0	No	Yes
M7	0	0	1	0	0	0	No	Yes
M8	0	0	1	0	0	0	Yes	No
M9	0	0	1	1	1	1	Yes	No
MA	1	0	0	0	0	0	No	No
MC	1	0	0	0	0	0	Yes	No
ME	1	0	0	0	0	0	No	No
MH	1	0	0	0	1	0	Yes	No
MJ	1	0	0	0	0	0	No	Yes
MK	1	0	1	0	0	0	Yes	No
ML	1	0	0	1	0	0	No	Yes
MM	0	1	0	0	0	0	No	Yes
MN	1	0	0	0	0	0	Yes	No
MP	1	0	0	0	0	0	Yes	No
MT	1	0	0	0	0	0	Yes	No
MX	1	1	0	0	1	0	No	Yes
N0	0	0	1	1	1	0	Yes	No
N1	0	0	1	1	1	1	No	Yes
N2	0	0	1	1	1	1	Yes	No
N3	0	0	1	1	0	1	Yes	No
N5	0	0	1	0	0	0	No	No
N6	0	0	1	1	1	1	No	Yes
N7	0	0	1	0	0	0	Yes	No
N8	0	0	1	1	1	1	No	No
N9	0	0	1	1	1	1	No	Yes
NA	1	0	0	0	1	0	No	Yes
NC	1	1	0	1	1	1	Yes	No
NE	1	1	0	0	0	0	Yes	No
NH	1	0	0	0	1	0	No	Yes
NJ	1	0	0	0	0	0	Yes	No
NK	0	1	0	1	0	1	Yes	No
NL	0	1	0	0	0	1	No	Yes
NM	0	1	0	1	1	1	No	Yes
NN	0	1	0	0	0	0	Yes	No
NP	0	1	0	0	0	1	No	Yes

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
NT	0	1	1	1	1	1	No	No
NU	0	1	0	0	0	0	No	Yes
NV	0	1	1	0	0	1	Yes	No
NX	0	1	0	0	0	0	No	Yes
NY	0	1	1	0	1	0	No	No
P0	0	0	1	1	1	1	No	Yes
P1	0	0	1	0	0	0	No	Yes
PA	0	1	0	0	1	0	Yes	No
PC	0	1	0	0	1	0	No	Yes
PE	0	1	1	0	1	1	No	No
PH	0	1	0	0	0	0	No	Yes
PJ	0	1	1	0	0	0	No	Yes
PK	0	1	0	0	0	0	No	Yes
PL	0	1	0	0	0	1	No	No
PM	0	1	0	0	1	0	No	Yes
PN	0	1	1	1	1	0	No	No
PP	0	1	0	0	1	0	Yes	No
PT	0	1	0	1	1	1	No	No
PU	0	1	1	0	0	0	Yes	No
PV	0	1	0	1	0	0	Yes	No
PX	0	1	1	0	1	0	No	Yes
PY	0	1	0	0	0	0	No	Yes
T0	0	0	1	1	0	0	No	Yes
T1	0	0	1	1	1	1	Yes	No
T2	0	0	1	0	1	1	Yes	No
T3	0	0	1	1	1	1	No	Yes
T4	0	0	1	0	0	0	No	Yes
T5	0	0	1	0	0	0	Yes	No
T6	0	0	1	0	1	1	No	No
T7	0	0	1	0	0	0	Yes	No
T8	0	0	1	0	0	0	No	No
T9	0	0	1	0	0	0	No	No
TA	0	1	1	0	0	0	Yes	No
TC	0	1	0	0	0	0	No	No
TE	0	1	0	0	0	0	No	Yes
TH	0	1	0	0	1	0	No	Yes
TJ	0	1	0	0	0	0	Yes	No
TK	0	1	0	0	0	0	No	Yes
TL	0	1	0	0	0	0	No	Yes
TM	0	1	0	1	1	1	No	Yes
TN	0	1	0	0	0	0	No	No
TP	0	1	1	0	1	0	No	No
TT	0	1	0	0	1	1	Yes	No
TU	0	1	0	1	0	0	No	Yes
TV	0	1	0	0	0	0	No	Yes
TX	0	1	0	0	0	0	Yes	No
TY	0	1	0	0	1	0	Yes	No
U0	0	0	1	1	0	0	No	Yes
U1	0	0	1	0	1	1	Yes	No
U2	0	0	1	1	1	0	No	Yes
U3	0	0	1	0	1	1	No	Yes
U4	0	0	1	1	1	1	No	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
U5	0	0	1	0	0	0	Yes	No
U6	0	0	1	0	0	0	No	Yes
U7	0	0	1	0	0	1	Yes	No
U8	0	0	1	0	0	0	No	Yes
U9	0	0	1	0	0	0	No	Yes
UA	0	1	0	0	0	1	Yes	No
UC	0	1	0	0	0	0	No	Yes
UE	0	1	0	0	0	0	Yes	No
UH	0	1	0	0	0	0	No	Yes
UJ	0	1	0	0	0	0	No	Yes
UK	0	1	1	0	0	0	No	Yes
UL	0	1	0	0	0	1	No	Yes
UM	0	1	0	1	0	1	Yes	No
UN	0	1	0	0	0	0	Yes	No
UP	0	1	1	0	1	1	No	Yes
UT	0	1	0	0	0	0	No	Yes
UU	0	1	1	0	1	1	No	No
UV	0	1	0	0	1	0	No	No
UX	0	1	0	0	1	1	No	Yes
UY	0	1	1	0	0	1	No	Yes
V0	0	0	1	0	0	0	No	Yes
V1	0	0	1	1	1	1	Yes	No
V2	0	0	1	0	1	1	Yes	No
V3	0	0	1	0	0	0	Yes	No
V4	0	0	1	1	1	1	Yes	No
V5	0	0	1	0	0	0	No	Yes
V6	0	0	1	1	1	1	No	Yes
V7	0	0	1	0	0	0	No	No
V8	0	0	1	1	1	1	Yes	No
V9	0	0	1	0	0	0	Yes	No
VA	0	1	0	0	0	1	No	No
VC	0	1	0	0	0	1	No	Yes
VE	0	1	1	0	1	1	No	Yes
VH	0	1	0	1	0	0	Yes	No
VJ	0	1	0	0	0	0	No	No
VK	0	1	1	0	1	1	No	Yes
VL	0	1	1	1	0	1	No	Yes
VM	0	1	0	0	0	0	No	Yes
VN	0	1	0	0	0	0	Yes	No
VP	0	1	0	1	1	0	Yes	No
VT	0	1	1	1	1	1	No	Yes
VU	0	1	0	1	1	0	No	Yes
VV	0	1	0	0	0	0	No	Yes
VX	0	1	0	1	0	1	Yes	No
VY	0	1	0	0	0	0	Yes	No
X1	0	0	1	1	1	1	Yes	No
X2	0	0	1	0	0	1	No	Yes
X3	0	0	1	1	0	1	Yes	No
X4	0	0	1	0	0	0	No	Yes
X5	0	0	1	0	0	0	No	No
X6	0	0	1	1	1	0	No	Yes
X7	0	0	1	1	1	1	No	No

TABLE HIV (CONTINUED)

Flag	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	Male	Female
X8	0	0	1	1	1	1	No	Yes
X9	0	0	1	1	1	0	Yes	No
XA	0	1	0	0	0	0	No	Yes
XC	0	1	0	1	0	1	No	Yes
XE	0	1	0	0	0	0	No	Yes
XH	0	1	0	1	1	1	No	Yes
XJ	0	1	1	1	1	1	Yes	No
XK	0	1	0	0	0	0	Yes	No
XL	0	1	0	0	0	0	Yes	No
XM	0	1	0	1	0	1	Yes	No
XN	0	1	1	1	1	1	No	No
XP	0	1	0	1	0	0	No	No
XT	0	1	0	0	0	1	No	Yes
XU	0	1	0	0	0	1	Yes	No
XV	0	1	0	0	0	0	Yes	No
XX	0	1	0	1	0	1	No	Yes
XY	0	1	0	0	0	1	No	No
Y0	0	0	1	0	1	1	Yes	No
Y1	0	0	1	1	0	1	No	No
Y2	0	0	1	0	0	1	No	No
Y3	0	0	1	1	1	0	No	Yes
Y4	0	0	1	0	0	0	No	Yes
Y5	0	0	1	0	1	0	No	Yes
Y6	0	0	1	1	0	0	No	Yes
Y7	0	0	1	0	1	1	Yes	No
Y8	0	0	1	0	0	0	No	Yes
Y9	0	0	1	1	0	0	No	Yes
YA	0	1	0	0	0	1	Yes	No
YC	0	1	0	0	0	0	No	Yes
YE	0	1	0	0	0	1	No	Yes
YH	0	1	0	1	1	0	Yes	No
YJ	0	1	0	1	1	0	No	Yes
YK	0	1	0	0	0	0	No	Yes
YL	0	1	1	0	0	0	No	Yes
YM	0	1	0	0	0	0	No	No
YN	0	1	0	1	1	1	Yes	No
YP	0	1	0	1	1	0	Yes	No
YT	0	1	0	1	0	0	Yes	No
YU	0	1	0	0	1	1	No	Yes
YV	0	1	0	1	1	1	No	Yes
YX	0	1	0	0	0	0	No	No
YY	0	1	0	0	0	1	No	No

Table HV. Encounter histories of Hudsonian Godwits (*Limosa haemastica*) for within season survival on the non-breeding grounds during the 2009 – 2010 season on Chiloé Island, Chile. Period 1 spanned three survey days (7 – 9 January) at Pullao (n = 126 observations). Period 2 spanned three survey days (10 – 12 January) at Ten-Ten (n = 16 observations) and Pullao (n = 152 observations). Period 3 spanned four survey days (13, 15, 16, and 19 January) at Pullao (n = 109 observation), Curaco de Vélez (n = 18 observations), Teguel (n = 6 observations), and Putemún (n = 3 observations). Period 4 was if the individual was seen at any time during the 2010 – 2011 non-breeding season. A "1" denotes the individuals was seen or re-captured during that non-breeding season, and a "0" specifies the individual was not seen.

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
0	0	1	0	0	Yes	No
1	1	1	1	1	No	Yes
8	0	1	0	1	Yes	No
50	1	1	1	0	No	Yes
51	0	1	0	1	Yes	No
52	1	1	0	1	No	Yes
58	0	1	1	1	Yes	No
61	0	1	1	1	No	Yes
67	1	0	1	1	No	Yes
68	1	1	0	1	Yes	No
71	1	0	0	1	No	Yes
72	0	0	1	0	Yes	No
81	1	1	1	1	Yes	No
82	1	1	1	1	No	Yes
87	1	0	1	1	No	No
88	1	1	1	1	No	Yes
90	1	0	1	1	Yes	No
91	0	1	1	1	No	Yes
92	1	1	1	1	Yes	No
A3	0	0	1	1	Yes	No
A4	1	1	1	1	No	Yes
A5	1	0	1	1	No	Yes
A7	1	1	1	1	Yes	No
AAC	1	0	1	1	No	Yes
AAL	1	0	0	1	No	Yes
AAP	1	1	0	1	No	Yes
AAU	1	1	1	1	No	Yes
ACA	1	1	1	1	No	No
ACC	0	1	0	1	No	No
ACH	0	0	1	1	Yes	No
ACJ	0	1	0	0	Yes	No
ACM	0	1	1	0	No	No
ACT	0	1	1	1	No	Yes
AEA	0	0	1	0	No	Yes
AEH	1	0	0	1	No	Yes
AEK	1	1	1	1	No	Yes
AEN	0	0	1	0	No	Yes
AEP	0	1	0	1	Yes	No
AEU	1	1	0	1	No	Yes
AEY	1	1	0	1	No	No
AHC	1	1	0	0	Yes	No
AHH	0	1	0	0	No	No
AHM	0	1	1	0	Yes	No
AHP	1	1	1	1	Yes	No
AHY	0	1	0	0	No	Yes
AJA	1	0	1	1	No	No
AJC	1	1	1	1	Yes	No
AJH	1	1	1	1	No	Yes
AJL	1	1	1	1	Yes	No
AJN	1	0	0	0	No	Yes
AJP	1	0	1	1	No	No
AJT	1	0	1	1	No	Yes

TABLE HV (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
AJX	0	1	0	0	No	Yes
AKA	0	1	0	1	No	No
AKC	1	1	1	1	No	No
AKE	1	1	1	1	Yes	No
AL	1	0	0	0	No	Yes
ALA	1	0	1	1	No	Yes
ALH	0	0	1	1	Yes	No
ALK	0	1	0	1	Yes	No
ALN	1	1	1	1	No	Yes
ALP	0	0	1	0	Yes	No
ALY	0	1	0	0	No	Yes
AMA	1	1	1	1	No	No
AMC	0	0	1	1	No	No
AME	0	1	0	1	No	Yes
AMH	1	1	1	1	No	No
AMK	0	1	0	1	Yes	No
AML	1	0	0	1	Yes	No
AMM	1	0	1	1	Yes	No
AMT	0	1	0	1	Yes	No
AMU	0	1	0	1	No	Yes
AMV	0	1	1	1	Yes	No
AMY	0	1	0	0	No	No
ANA	0	1	0	0	No	No
ANC	1	0	0	1	Yes	No
ANJ	1	1	1	0	No	Yes
ANK	1	1	1	1	Yes	No
ANL	1	1	1	1	No	Yes
ANN	0	0	1	1	No	Yes
ANP	0	1	0	1	Yes	No
ANV	1	1	1	1	Yes	No
ANY	0	1	1	1	No	No
APA	0	1	1	1	No	No
APC	0	0	1	1	Yes	No
AX	1	1	1	1	No	No
C2	0	1	1	1	Yes	No
C3	1	0	1	1	No	No
CJ	1	1	1	1	No	No
CM	1	1	0	1	No	No
CU	0	0	1	1	No	Yes
E1	1	1	1	0	Yes	No
E9	1	0	0	1	No	No
EH	1	1	0	1	Yes	No
EL	0	1	0	1	No	Yes
ET	0	1	0	0	Yes	No
EX	0	1	0	1	Yes	No
H0	0	1	1	1	Yes	No
H8	0	0	1	0	Yes	No
H9	0	0	1	1	Yes	No
HE	1	1	1	0	No	Yes
HL	0	1	0	1	Yes	No

TABLE HV (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
HX	1	1	0	0	No	Yes
HY	0	0	1	0	No	No
JJ	1	1	0	1	No	No
JP	0	0	1	1	Yes	No
JT	1	1	0	1	No	Yes
JU	0	1	0	0	No	Yes
K6	0	1	0	1	No	Yes
K9	1	1	0	1	No	Yes
KJ	0	1	1	1	Yes	No
KL	1	1	1	1	No	Yes
KN	0	1	0	0	No	Yes
L9	0	1	0	0	No	Yes
LC	1	1	0	1	No	Yes
LL	1	1	0	1	No	Yes
LN	0	0	1	1	No	No
LV	1	0	1	1	Yes	No
M1	0	0	1	1	No	No
M2	0	1	0	1	No	Yes
M4	0	1	0	1	No	Yes
M6	0	1	0	0	No	Yes
M9	1	1	1	1	Yes	No
ML	0	0	1	0	No	Yes
N0	0	1	1	1	Yes	No
N1	1	1	1	1	No	Yes
N2	0	1	1	1	Yes	No
N3	0	1	0	1	Yes	No
N6	0	1	0	1	No	Yes
N8	0	1	1	1	No	No
N9	0	0	1	1	No	Yes
NC	0	1	1	1	Yes	No
NK	1	1	0	1	Yes	No
NM	1	1	1	1	No	Yes
NT	1	0	0	1	No	No
P0	0	1	0	1	No	Yes
PN	0	0	1	1	No	No
PT	0	1	0	1	No	No
PV	0	1	0	0	Yes	No
T0	1	1	0	0	No	Yes
T1	1	0	1	1	Yes	No
T3	0	1	0	1	No	Yes
TM	1	1	0	1	No	Yes
TU	1	0	0	0	No	Yes
U0	1	0	0	0	No	Yes
U2	0	1	0	1	No	Yes
U4	0	1	1	1	No	No
UM	0	0	1	1	Yes	No
V1	1	1	1	1	Yes	No
V4	0	1	1	1	Yes	No
V6	0	0	1	1	No	Yes
V8	1	1	1	1	Yes	No

TABLE HV (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
VH	1	0	0	0	Yes	No
VL	0	0	1	1	No	Yes
VP	0	1	1	1	Yes	No
VT	1	1	0	1	No	Yes
VU	1	1	0	1	No	Yes
VX	0	1	0	1	Yes	No
X0	1	0	0	0	No	Yes
X1	1	0	0	1	Yes	No
X3	1	1	0	1	Yes	No
X6	0	1	0	1	No	Yes
X7	1	1	1	1	No	No
X8	1	0	1	1	No	Yes
X9	0	0	1	1	Yes	No
XC	0	1	1	1	No	Yes
XH	0	1	0	1	No	Yes
XJ	0	1	0	1	Yes	No
XM	0	1	1	1	Yes	No
XN	0	1	0	1	No	No
XP	0	1	0	0	No	No
XX	0	1	0	1	No	Yes
Y1	0	1	0	1	No	No
Y3	0	1	1	1	No	Yes
Y6	0	1	0	0	No	Yes
Y9	0	1	1	0	No	Yes
YH	0	1	0	1	Yes	No
YJ	1	0	0	1	No	Yes
YN	1	1	0	1	Yes	No
YP	1	1	0	1	Yes	No
YT	1	0	0	0	Yes	No
YV	1	1	0	1	No	Yes

Table HVI. Encounter histories of Hudsonian Godwits (*Limosa haemastica*) for within season survival on the non-breeding grounds during the 2010 – 2011 season on Chiloé Island, Chile. Period 1 spanned four survey days (5 – 8 January) at Pullao (n = 224 observations), at Putemún (n = 6 observations), and at Curaco de Vélez (n = 8 observations). Period 2 spanned four survey days (9 – 12 January) at Rilán (n = 68 observations), Pullao (n = 90 observations), Curaco de Vélez (n = 24 observations), and Putemún (n = 109 observations). Period 3 spanned four survey days (13, 15, 16, and 17 January) at Pullao (n = 235 observation), Curaco de Vélez (n = 10 observations), Chúllec (n = 2 observations), Rilán (n = 46 observations), and Putemún (n = 145 observations). Period 4 was if the individual was seen at any time during the 2011 – 2012 non-breeding season. A "1" denotes the individuals was seen or re-captured during that non-breeding season, and a "0" specifies the individual was not seen.

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
1	0	1	1	1	No	Yes
4	0	1	1	1	No	Yes
8	1	1	0	0	Yes	No
10	1	1	0	0	No	No
25	0	1	0	1	No	No
52	0	1	0	1	No	Yes
57	0	1	0	0	Yes	No
58	0	0	1	1	Yes	No
60	1	0	1	0	Yes	No
61	1	1	1	1	No	Yes
62	1	1	1	1	No	Yes
67	1	1	1	1	No	Yes
68	1	1	1	0	Yes	No
69	1	0	1	1	No	Yes
71	0	1	1	1	No	Yes
78	1	1	1	1	Yes	No
81	1	1	1	0	Yes	No
82	0	1	1	1	No	Yes
83	1	0	0	0	No	Yes
85	1	0	0	1	No	Yes
87	0	1	1	0	No	No
88	1	1	1	1	No	Yes
90	1	1	1	1	Yes	No
91	1	1	1	0	No	Yes
92	1	0	1	0	Yes	No
A2	1	0	0	0	No	Yes
A3	1	1	1	1	Yes	No
A4	1	1	1	1	No	Yes
A5	0	1	0	1	No	Yes
A7	1	1	1	0	Yes	No
AAH	0	1	1	1	Yes	No
AAL	0	1	1	1	No	Yes
AAN	0	1	1	1	No	Yes
AAP	0	0	1	0	No	Yes
AAU	1	1	1	1	No	Yes
AAY	0	1	0	1	No	No
ACA	1	1	1	1	No	No
ACC	1	1	1	1	No	No
ACH	1	1	1	0	Yes	No
ACK	0	1	1	1	Yes	No
ACL	0	1	1	0	Yes	No
ACP	0	1	0	1	Yes	No
ACT	1	1	1	0	No	Yes
ACV	1	1	1	1	No	No
ACX	0	1	1	0	Yes	No
ACY	0	1	1	0	Yes	No
AEH	1	0	0	1	No	Yes
AEJ	1	0	0	1	No	No
AEK	1	1	1	1	No	Yes
AEP	0	0	1	1	Yes	No
AEU	0	1	1	1	No	Yes
AEV	1	1	1	1	No	No

TABLE HVI (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
AEX	0	0	1	0	No	No
AEY	1	1	1	1	No	No
AHJ	1	0	0	0	No	No
AHL	1	1	1	1	Yes	No
AHP	1	1	1	1	Yes	No
AHT	0	0	1	1	Yes	No
AHU	0	0	1	1	Yes	No
AHV	0	1	0	0	No	Yes
AHX	1	0	0	0	No	Yes
AJA	1	1	1	1	No	No
AJC	1	1	1	1	Yes	No
AJH	0	1	1	0	No	Yes
AJJ	0	1	0	0	No	Yes
AJL	1	0	1	1	Yes	No
AJP	0	1	1	1	No	No
AJT	1	1	0	0	No	Yes
AJU	0	1	1	1	No	No
AKA	0	1	1	1	No	No
AKC	1	1	0	1	No	No
AKE	1	1	1	1	Yes	No
AKK	1	0	0	0	No	No
AKL	1	0	1	1	Yes	No
AKM	1	1	1	1	Yes	No
AKN	1	1	1	1	No	No
AKT	1	1	0	1	No	Yes
AKU	1	0	0	1	No	Yes
AKV	1	1	1	0	No	Yes
AKX	0	0	1	1	No	Yes
AKY	1	1	1	0	No	Yes
ALA	1	1	1	1	No	Yes
ALH	0	0	1	1	Yes	No
ALK	1	1	1	1	Yes	No
ALM	1	1	1	1	No	Yes
ALN	1	1	1	1	No	Yes
ALU	1	0	1	0	Yes	No
ALX	1	1	1	1	Yes	No
AMA	0	1	1	1	No	No
AMC	1	1	1	1	No	No
AME	0	1	1	1	No	Yes
AMH	1	0	1	1	No	No
AML	1	1	1	1	Yes	No
AMM	1	1	1	1	Yes	No
AMN	1	0	0	1	No	Yes
AMP	1	1	0	1	Yes	No
AMT	1	1	1	1	Yes	No
AMU	0	0	1	0	No	Yes
AMV	1	1	0	0	Yes	No
AMY	0	1	0	0	No	No
ANC	1	1	0	1	Yes	No
ANK	1	1	1	1	Yes	No

TABLE HVI (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
ANL	0	1	1	0	No	Yes
ANM	0	0	1	0	No	No
ANN	0	1	1	0	No	Yes
ANP	0	0	1	1	Yes	No
ANU	1	1	1	1	Yes	No
ANV	1	1	1	1	Yes	No
ANY	0	1	1	1	No	No
APA	0	1	1	0	No	No
APC	1	1	1	1	Yes	No
APK	1	0	0	0	No	Yes
APN	1	0	1	1	No	Yes
APT	0	1	1	1	No	No
APU	1	0	1	0	No	Yes
APV	1	0	0	1	No	Yes
APY	0	0	1	1	No	Yes
ATA	1	0	0	0	No	No
ATE	1	0	0	0	No	Yes
ATH	0	1	0	1	No	Yes
ATJ	1	1	1	1	No	Yes
ATL	1	1	1	1	No	Yes
ATM	1	1	1	1	No	Yes
ATN	1	1	1	1	No	Yes
ATP	1	1	1	1	No	No
ATT	1	0	1	1	No	No
ATU	1	1	0	0	Yes	No
ATV	1	1	1	1	No	No
ATX	1	1	0	1	Yes	No
ATY	1	1	1	1	No	Yes
AUK	1	0	0	0	No	No
AUT	1	0	0	1	Yes	No
AUU	0	1	0	0	No	Yes
AUV	1	1	1	1	No	Yes
AUX	1	0	0	0	No	No
AVK	1	0	0	1	No	Yes
AVL	1	0	1	1	No	Yes
AVU	0	1	1	0	No	Yes
AX	0	1	1	1	No	No
AXE	0	1	1	0	No	Yes
AXH	1	0	0	0	No	Yes
AXL	0	1	1	1	No	Yes
AXX	1	1	0	1	Yes	No
AXY	1	1	0	1	Yes	No
AYA	0	0	1	0	No	No
AYC	0	0	1	1	No	Yes
AYE	0	1	0	1	No	Yes
AYH	1	1	1	0	Yes	No
AYL	0	1	1	1	No	Yes
AYM	1	1	1	1	Yes	No
AYN	1	0	0	0	No	Yes
AYU	0	1	1	1	No	Yes

TABLE HVI (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
AYV	0	0	1	1	Yes	No
AYY	0	1	1	1	Yes	No
C1	0	1	0	1	No	Yes
C2	0	1	1	1	Yes	No
C3	1	1	1	1	No	No
CA	1	0	0	1	Yes	No
CAA	1	0	0	1	No	Yes
CAC	1	1	0	0	No	Yes
CAK	1	1	1	1	No	Yes
CAL	1	0	0	1	No	Yes
CAM	1	0	1	1	Yes	No
CAN	1	0	0	0	No	Yes
CAT	1	0	0	1	No	No
CAU	1	1	1	0	Yes	No
CAV	1	1	0	0	No	Yes
CAX	1	1	1	0	Yes	No
CCA	1	1	1	1	No	Yes
CCC	1	1	1	1	Yes	No
CCE	1	1	1	0	No	Yes
CCH	0	1	1	0	Yes	No
CCJ	1	1	1	1	No	No
CCK	1	1	1	1	No	Yes
CCL	1	1	1	1	Yes	No
CCN	1	1	1	1	No	Yes
CCP	1	1	1	1	No	Yes
CCU	1	1	1	1	No	No
CCV	1	1	1	1	No	Yes
CCY	1	0	0	1	No	Yes
CH	1	0	0	0	No	No
CHE	1	1	1	0	No	Yes
CHJ	1	1	1	1	No	Yes
CHK	1	0	1	0	Yes	No
CHP	1	1	1	1	No	Yes
CHU	1	1	1	1	No	Yes
CHV	1	0	0	0	No	Yes
CHY	1	0	0	1	No	Yes
CJ	1	1	1	1	No	No
CM	1	0	1	1	No	No
CT	0	0	1	0	No	Yes
CU	0	1	0	0	No	Yes
CV	0	1	1	1	Yes	No
CX	0	1	0	0	No	No
E2	0	1	1	0	No	Yes
E4	0	0	1	0	No	Yes
E9	0	1	1	0	No	No
EH	1	1	1	1	Yes	No
EL	1	0	0	1	No	Yes
EX	1	1	1	1	Yes	No
H0	0	1	1	1	Yes	No
H1	1	1	0	0	Yes	No

TABLE HVI (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
H9	0	1	1	0	Yes	No
HA	0	1	0	0	No	Yes
HH	1	0	0	0	Yes	No
HL	1	0	1	0	Yes	No
HN	1	1	1	0	Yes	No
HU	1	1	0	0	Yes	No
J3	1	1	0	1	No	Yes
J4	0	0	1	1	No	No
J8	1	0	0	0	No	Yes
JJ	0	1	1	1	No	No
JP	1	1	1	1	Yes	No
JT	1	0	0	1	No	Yes
K0	0	1	1	0	No	Yes
K1	0	1	0	1	Yes	No
K6	1	0	0	0	No	Yes
K8	0	1	1	1	No	Yes
K9	1	0	0	1	No	Yes
KC	0	1	0	1	No	Yes
KH	1	0	1	0	No	Yes
KJ	1	0	1	0	Yes	No
KL	1	1	1	1	No	Yes
L0	1	1	1	1	Yes	No
L4	0	0	1	0	Yes	No
LH	0	1	1	1	No	No
LL	0	1	0	1	No	Yes
LN	1	1	1	0	No	No
LP	0	1	1	0	No	No
LT	0	1	1	1	Yes	No
LU	0	1	1	1	Yes	No
LV	0	1	1	1	Yes	No
M0	1	1	0	1	No	Yes
M1	1	0	0	0	No	No
M3	0	0	1	1	Yes	No
M4	0	1	0	1	No	Yes
M5	0	1	1	0	No	Yes
M9	1	1	0	1	Yes	No
MH	0	1	0	0	Yes	No
MX	0	1	1	0	No	Yes
N0	0	0	1	0	Yes	No
N1	1	1	1	1	No	Yes
N2	1	1	1	1	Yes	No
N6	0	1	1	1	No	Yes
N8	1	1	1	1	No	No
N9	1	1	1	1	No	Yes
NA	0	0	1	0	No	Yes
NC	0	1	1	1	Yes	No
NH	1	0	1	0	No	Yes
NM	0	0	1	1	No	Yes
NT	1	0	1	1	No	No
NY	0	0	1	0	No	No

TABLE HVI (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
P0	1	0	0	1	No	Yes
PA	0	1	0	0	Yes	No
PC	0	0	1	0	No	Yes
PE	1	1	1	1	No	No
PM	1	0	0	0	No	Yes
PN	1	0	0	0	No	No
PP	0	0	1	0	Yes	No
PT	0	1	1	1	No	No
PX	1	1	0	0	No	Yes
T1	0	0	1	1	Yes	No
T2	1	1	1	1	Yes	No
T3	1	0	0	1	No	Yes
T6	0	1	0	1	No	No
TH	1	0	0	0	No	Yes
TM	1	0	1	1	No	Yes
TP	0	1	0	0	No	No
TT	1	0	0	1	Yes	No
TY	0	1	0	0	Yes	No
U1	1	0	0	1	Yes	No
U2	1	0	0	0	No	Yes
U3	0	1	0	1	No	Yes
U4	1	1	1	1	No	No
UP	0	1	0	1	No	Yes
UU	1	0	1	1	No	No
UV	1	0	1	0	No	No
UX	1	0	0	1	No	Yes
V1	1	1	1	1	Yes	No
V2	1	1	1	1	Yes	No
V4	1	1	1	1	Yes	No
V6	0	1	1	1	No	Yes
V8	1	1	1	1	Yes	No
VE	0	0	1	1	No	Yes
VK	0	0	1	1	No	Yes
VP	0	0	1	0	Yes	No
VT	0	1	1	1	No	Yes
VU	0	1	1	0	No	Yes
X1	0	1	1	1	Yes	No
X6	1	0	0	0	No	Yes
X7	0	1	1	1	No	No
X8	1	1	1	1	No	Yes
X9	1	1	1	0	Yes	No
XH	1	0	0	1	No	Yes
XJ	0	0	1	1	Yes	No
XN	0	0	1	1	No	No
Y0	0	1	1	1	Yes	No
Y3	1	1	1	0	No	Yes
Y5	0	1	0	0	No	Yes
Y7	1	0	1	1	Yes	No
YH	1	0	0	0	Yes	No
YJ	0	1	0	0	No	Yes

TABLE HVI (CONTINUED)

Flag	PER 1	PER 2	PER 3	PER 4	Male	Female
YN	1	0	1	1	Yes	No
YP	0	1	1	0	Yes	No
YU	1	0	1	1	No	Yes

Table HVII. Encounter histories for annual survival of Hudsonian Godwits (*Limosa haemastica*) on the breeding grounds at Beluga River, Alaska from 2009 – 2017. A "1" denotes the individuals was seen or captured during that breeding season, and a "0" specifies the individual was either not seen or had not yet been marked.

ID	2009	2010	2011	2012	2014	2015	2016	2017	Male	Female
1000	1	1	1	1	1	0	0	0	No	Yes
1001	1	0	0	0	0	0	0	0	No	Yes
1002	1	1	1	1	1	0	0	0	No	Yes
1003	1	0	0	0	0	0	0	0	No	Yes
1004	1	0	0	0	0	0	0	0	No	Yes
1005	1	1	0	0	0	0	0	0	Yes	No
1006	1	0	0	0	0	0	0	0	No	Yes
1007	1	0	0	0	0	0	0	0	No	Yes
1008	1	0	0	0	0	0	0	0	No	Yes
1009	1	1	1	1	1	1	1	0	No	Yes
1010	1	1	1	1	0	0	0	0	Yes	No
1011	1	1	1	1	1	1	1	0	No	Yes
1012	1	1	1	1	0	0	0	0	Yes	No
1013	1	1	0	0	0	0	0	0	No	Yes
1014	1	0	0	0	0	0	0	0	No	Yes
1015	1	1	1	1	1	1	0	0	No	Yes
1016	1	1	1	1	0	0	0	0	Yes	No
1017	1	1	1	1	0	0	0	0	Yes	No
1018	1	1	1	1	0	0	0	0	No	Yes
1019	1	0	0	0	0	0	0	0	Yes	No
1020	1	1	1	1	0	0	0	0	Yes	No
1021	1	1	1	1	0	0	0	0	Yes	No
1022	1	0	0	0	0	0	0	0	No	Yes
1023	1	1	0	0	0	0	0	0	No	Yes
1024	1	1	1	0	0	0	0	0	No	Yes
1025	1	0	0	0	0	0	0	0	Yes	No
1026	1	1	1	1	0	0	0	0	Yes	No
1027	1	1	1	1	1	1	0	0	Yes	No
1028	1	0	0	0	0	0	0	0	Yes	No
1029	1	1	1	1	1	1	0	0	Yes	No
1030	1	1	1	1	1	0	0	1	Yes	No
1031	1	0	0	0	0	0	0	0	Yes	No
1032	1	1	1	1	1	1	0	0	No	Yes
1033	1	1	1	1	1	1	1	1	No	Yes
1034	1	1	1	1	1	1	1	0	Yes	No
1035	1	1	1	1	0	0	0	0	Yes	No
1036	1	0	0	0	0	0	0	0	Yes	No
1037	1	1	1	1	0	0	0	0	No	Yes
1044	1	1	1	1	1	0	0	0	No	Yes
1056	0	0	0	1	1	1	1	0	No	Yes
1059	0	0	0	0	1	0	0	0	Yes	No
1062	1	1	1	1	1	1	0	0	Yes	No
1064	1	0	0	0	0	0	0	0	Yes	No
1069	0	0	0	0	1	0	0	0	Yes	No
1106	0	1	1	1	0	0	0	0	No	Yes
1107	0	1	1	1	0	0	0	0	No	Yes
1108	0	1	1	1	1	1	1	0	Yes	No
1109	0	1	1	1	1	1	1	0	Yes	No
1110	0	1	0	0	0	0	0	0	Yes	No
1111	0	1	1	0	0	0	0	0	No	Yes
1112	0	1	1	1	1	0	0	0	No	Yes
1113	0	1	1	1	1	1	1	0	No	Yes

TABLE HVII (CONTINUED)

ID	2009	2010	2011	2012	2014	2015	2016	2017	Male	Female
1114	0	1	0	0	0	0	0	0	Yes	No
1115	0	1	0	0	0	0	0	0	No	Yes
1116	0	1	1	1	1	0	0	0	No	Yes
1136	0	1	0	0	0	0	0	0	No	Yes
1137	0	1	1	1	1	1	1	1	Yes	No
1146	0	1	1	0	0	0	0	0	No	Yes
1147	0	1	1	1	0	0	0	0	Yes	No
1166	0	1	1	1	1	1	0	0	Yes	No
1180	0	0	1	1	0	0	0	0	No	Yes
1181	0	0	1	1	1	0	0	0	Yes	No
1182	0	0	1	1	0	0	0	0	No	Yes
1183	0	0	1	1	0	0	0	0	Yes	No
1184	0	0	1	1	0	0	0	0	Yes	No
1185	0	0	1	1	0	0	0	0	Yes	No
1186	0	0	1	0	0	0	0	0	No	Yes
1187	0	0	1	1	0	0	0	0	Yes	No
1188	0	0	1	0	0	0	0	0	Yes	No
1189	0	0	1	0	0	0	0	0	No	Yes
1190	0	0	1	1	1	0	0	0	No	Yes
1191	0	0	1	1	1	1	1	1	Yes	No
1192	0	0	1	0	0	0	0	0	Yes	No
1193	0	0	1	0	0	0	0	0	No	Yes
1194	0	0	1	1	1	1	1	1	Yes	No
1195	0	0	1	1	0	0	0	0	No	Yes
1196	0	0	1	1	0	0	0	0	Yes	No
1212	0	0	0	0	1	0	0	0	No	Yes
1229	0	0	1	0	0	0	0	0	No	Yes
1246	0	0	0	0	1	1	1	0	Yes	No
1277	0	0	0	1	0	0	0	0	No	Yes
1278	0	0	0	1	1	0	0	0	Yes	No
1279	0	0	0	1	1	1	1	0	Yes	No
1280	0	0	0	1	1	1	1	0	No	Yes
1281	0	0	0	1	1	0	0	0	No	Yes
1282	0	0	0	1	1	0	0	0	Yes	No
1283	0	0	0	1	0	0	0	0	No	Yes
1284	0	0	0	1	1	0	0	0	No	Yes
1285	0	0	0	1	0	0	0	0	No	Yes
1286	0	0	0	1	0	0	0	0	Yes	No
1287	0	0	0	1	1	1	0	0	Yes	No
1288	0	0	0	1	1	1	1	0	No	Yes
1289	0	0	0	1	1	0	0	0	No	Yes
1299	0	0	0	0	1	0	0	0	No	Yes
1300	0	0	0	0	1	1	1	0	No	Yes
1301	0	0	0	0	1	1	1	0	No	Yes
1302	0	0	0	0	1	1	1	0	Yes	No
1303	0	0	0	0	1	0	0	0	Yes	No
1304	0	0	0	0	1	1	1	1	Yes	No
1305	0	0	0	0	1	1	1	0	No	Yes
1314	0	0	0	0	1	1	1	1	Yes	No
1323	0	0	0	0	1	1	0	0	No	Yes

TABLE HVII (CONTINUED)

ID	2009	2010	2011	2012	2014	2015	2016	2017	Male	Female
1335	0	0	0	0	0	1	1	0	No	Yes
1336	0	0	0	0	0	1	1	1	No	Yes
1337	0	0	0	0	0	1	1	1	No	Yes
1338	0	0	0	0	0	1	1	0	Yes	No
1339	0	0	0	0	0	1	1	1	Yes	No
1340	0	0	0	0	0	1	0	1	No	Yes
1341	0	0	0	0	0	1	1	0	No	Yes
1342	0	0	0	0	0	1	1	1	No	Yes
1343	0	0	0	0	0	1	1	0	No	Yes
1344	0	0	0	0	0	1	0	0	No	Yes
1345	0	0	0	0	0	1	1	1	Yes	No
1346	0	0	0	0	0	1	0	0	Yes	No
1347	0	0	0	0	0	1	1	1	Yes	No
1379	0	0	0	0	0	1	1	0	Yes	No
1403	0	0	0	0	0	0	1	1	Yes	No
1411	0	0	0	0	0	0	1	1	No	Yes

Table HVIII. Encounter histories of Hudsonian Godwits (*Limosa haemastica*) for within season survival during the breeding season at Beluga River, Alaska from 2009 – 2016. Period 1 is from 1 – 7 May, Period 2 is from 8 – 14 May, Period 3 is from 15 – 21 May, Period 4 is from 22 – 28 May, Period 5 is from 29 May – 4 June, and Period 6 is from 5 June – 16 July.

ID	PER 1	PER 2	PER 3	PER 4	PER 5	Male	Female
1010	0	0	1	0	1	Yes	No
1062	0	0	0	0	1	Yes	No
1033	0	0	0	1	1	No	Yes
1022	0	0	0	1	1	No	Yes
1032	0	0	0	1	1	No	Yes
1044	0	0	0	0	1	No	Yes
1028	0	1	1	1	1	Yes	No
1026	0	1	0	1	1	Yes	No
1024	0	0	0	1	1	No	Yes
1037	0	0	0	0	1	No	Yes
1035	0	0	0	1	1	Yes	No
1025	0	0	1	1	0	Yes	No
1034	0	0	0	1	1	Yes	No
1023	0	0	0	1	1	No	Yes
1029	0	0	0	1	1	Yes	No
1036	0	1	1	1	1	Yes	No
1021	0	0	0	1	1	Yes	No
1011	0	1	1	1	1	No	Yes
1020	0	0	1	1	0	Yes	No
1008	0	0	1	1	1	No	Yes
1030	0	0	0	1	0	Yes	No
1000	0	1	0	0	1	No	Yes
1031	0	0	0	1	1	Yes	No
1064	0	0	0	0	1	Yes	No
1017	0	0	1	0	0	Yes	No
1006	0	1	1	0	1	No	Yes
1014	0	0	1	0	1	No	Yes
1013	0	1	1	1	1	No	Yes
1004	0	1	1	0	1	No	Yes
1018	0	0	1	1	1	No	Yes
1009	0	1	1	0	0	No	Yes
1019	0	1	1	0	0	Yes	No
1002	0	1	1	0	0	No	Yes
1003	0	1	1	0	1	No	Yes
1016	0	0	1	0	1	Yes	No
1012	0	1	1	0	1	Yes	No
1001	0	1	1	1	0	No	Yes
1005	0	1	0	0	1	Yes	No
1007	0	1	1	0	0	No	Yes
1027	0	0	0	1	0	Yes	No
1015	0	0	1	1	1	No	Yes
1023	1	0	1	1	1	No	Yes
1112	0	1	0	1	0	No	Yes
1012	0	0	1	1	1	Yes	No
1005	1	1	0	1	1	Yes	No
1011	1	1	0	1	1	No	Yes
1108	0	0	1	1	0	Yes	No
1147	0	0	0	1	1	Yes	No
1109	0	0	1	1	0	Yes	No
1002	1	1	1	1	1	No	Yes
1114	0	0	0	1	0	Yes	No
1016	1	0	0	0	1	Yes	No

TABLE HVIII (CONTINUED)

ID	PER 1	PER 2	PER 3	PER 4	PER 5	Male	Female
1017	1	1	1	1	1	Yes	No
1062	0	1	1	1	1	Yes	No
1137	0	0	0	0	1	Yes	No
1030	0	0	1	0	1	Yes	No
1032	1	0	0	1	1	No	Yes
1107	0	0	1	1	1	No	Yes
1018	1	0	0	0	0	No	Yes
1111	0	0	1	1	1	No	Yes
1010	0	1	1	0	0	Yes	No
1115	0	0	0	1	0	No	Yes
1136	0	0	0	0	1	No	Yes
1116	0	0	1	0	1	No	Yes
1113	0	0	0	1	1	No	Yes
1029	1	1	1	0	0	Yes	No
1033	1	0	0	0	0	No	Yes
1000	1	1	1	1	1	No	Yes
1044	1	1	0	1	1	No	Yes
1024	1	0	0	0	0	No	Yes
1037	1	0	0	0	0	No	Yes
1013	0	0	0	0	1	No	Yes
1035	1	0	0	0	0	Yes	No
1020	1	0	0	0	0	Yes	No
1106	1	1	1	1	1	No	Yes
1026	1	0	0	1	1	Yes	No
1021	1	0	0	0	0	Yes	No
1110	0	0	1	1	0	Yes	No
1004	1	0	0	0	0	No	Yes
1009	1	0	0	0	0	No	Yes
1003	1	0	0	0	0	No	Yes
1027	0	1	1	1	0	Yes	No
1015	1	0	0	0	0	No	Yes
1027	0	0	0	0	1	Yes	No
1112	1	0	0	0	0	No	Yes
1190	0	0	0	1	1	No	Yes
1183	0	1	1	0	0	Yes	No
1012	0	1	1	0	0	Yes	No
1166	0	0	0	1	0	Yes	No
1021	0	0	1	0	1	Yes	No
1111	0	1	0	1	1	No	Yes
1107	1	1	1	1	1	No	Yes
1024	1	0	0	0	1	No	Yes
1108	0	1	1	0	1	Yes	No
1147	0	1	0	0	0	Yes	No
1180	0	1	1	1	1	No	Yes
1062	1	0	0	1	0	Yes	No
1184	0	0	1	0	1	Yes	No
1229	0	0	0	0	1	No	Yes
1189	0	0	0	1	1	No	Yes
1009	0	1	1	0	0	No	Yes
1196	0	0	0	0	1	Yes	No

TABLE HVIII (CONTINUED)

ID	PER 1	PER 2	PER 3	PER 4	PER 5	Male	Female
1191	0	0	0	1	1	Yes	No
1137	0	1	0	0	0	Yes	No
1188	0	0	0	1	1	Yes	No
1017	0	1	1	1	1	Yes	No
1192	0	0	0	0	1	Yes	No
1195	0	0	0	0	1	No	Yes
1182	0	1	1	1	1	No	Yes
1193	0	0	0	0	1	No	Yes
1109	1	0	0	1	0	Yes	No
1015	1	0	1	1	1	No	Yes
1029	0	1	1	0	1	Yes	No
1026	0	1	0	1	1	Yes	No
1194	0	0	0	0	1	Yes	No
1116	0	1	1	0	0	No	Yes
1030	1	0	0	0	0	Yes	No
1020	1	1	1	0	1	Yes	No
1033	1	0	0	1	1	No	Yes
1000	1	0	0	0	0	No	Yes
1011	0	1	1	1	1	No	Yes
1106	1	0	1	1	1	No	Yes
1037	1	0	0	1	1	No	Yes
1044	0	0	1	1	1	No	Yes
1186	0	0	1	1	0	No	Yes
1113	0	1	1	1	1	No	Yes
1002	0	0	1	1	1	No	Yes
1035	1	0	0	0	1	Yes	No
1032	0	0	1	1	1	No	Yes
1016	0	0	0	1	1	Yes	No
1018	0	0	1	1	1	No	Yes
1010	0	1	1	1	1	Yes	No
1181	0	1	1	1	1	Yes	No
1110	0	0	1	0	1	Yes	No
1185	0	0	1	1	0	Yes	No
1187	0	0	1	1	0	Yes	No
1277	0	1	1	1	1	No	Yes
1187	1	0	0	1	1	Yes	No
1284	0	0	0	1	1	No	Yes
1286	0	0	0	1	0	Yes	No
1279	0	0	1	1	1	Yes	No
1285	0	0	0	1	1	No	Yes
1282	0	0	0	1	1	Yes	No
1289	0	0	0	0	1	No	Yes
1278	0	1	1	0	0	Yes	No
1283	0	0	0	1	1	No	Yes
1027	1	0	0	0	1	Yes	No
1287	0	0	0	1	0	Yes	No
1009	0	1	0	1	1	No	Yes
1288	0	0	0	1	1	No	Yes
1280	0	0	1	1	1	No	Yes
1015	1	0	0	1	1	No	Yes

TABLE HVIII (CONTINUED)

ID	PER 1	PER 2	PER 3	PER 4	PER 5	Male	Female
1281	0	0	1	0	0	No	Yes
1113	0	1	0	1	1	No	Yes
1112	0	1	0	0	1	No	Yes
1011	0	0	1	1	1	No	Yes
1190	0	1	0	1	1	No	Yes
1183	0	1	0	1	0	Yes	No
1030	1	0	1	0	1	Yes	No
1012	0	1	1	1	0	Yes	No
1166	1	0	1	1	1	Yes	No
1062	1	0	1	1	0	Yes	No
1024	0	0	0	1	0	No	Yes
1108	0	0	0	1	1	Yes	No
1147	1	0	1	0	1	Yes	No
1180	0	1	0	0	0	No	Yes
1184	1	0	0	0	0	Yes	No
1196	0	1	0	1	1	Yes	No
1018	1	1	1	1	1	No	Yes
1017	1	0	1	0	1	Yes	No
1188	1	0	0	0	0	Yes	No
1192	1	0	0	0	0	Yes	No
1195	0	1	0	1	1	No	Yes
1002	0	0	1	0	0	No	Yes
1182	1	1	1	0	0	No	Yes
1191	1	0	0	1	1	Yes	No
1029	1	1	0	1	0	Yes	No
1026	1	1	0	0	0	Yes	No
1194	1	0	0	0	0	Yes	No
1116	1	1	1	1	1	No	Yes
1033	1	1	1	1	1	No	Yes
1020	0	1	1	1	1	Yes	No
1000	1	0	1	1	1	No	Yes
1109	1	0	1	0	0	Yes	No
1106	1	1	0	0	0	No	Yes
1037	1	0	0	1	1	No	Yes
1021	1	0	0	1	1	Yes	No
1035	1	1	1	1	1	Yes	No
1016	1	0	0	1	1	Yes	No
1010	0	1	1	1	1	Yes	No
1032	1	1	0	0	0	No	Yes
1056	1	0	0	1	1	No	Yes
1107	0	0	0	1	1	No	Yes
1044	1	0	0	1	1	No	Yes
1181	1	1	1	1	1	Yes	No
1305	0	1	1	1	1	No	Yes
1284	1	0	0	0	0	No	Yes
1279	1	1	1	1	1	Yes	No
1282	1	0	0	0	0	No	Yes
1289	1	1	0	0	1	No	Yes
1278	0	1	0	1	1	Yes	No
1027	1	0	1	1	1	Yes	No

TABLE HVIII (CONTINUED)

ID	PER 1	PER 2	PER 3	PER 4	PER 5	Male	Female
1287	0	0	1	1	0	Yes	No
1288	1	1	0	0	0	No	Yes
1280	0	0	0	0	1	No	Yes
1015	1	1	0	0	1	No	Yes
1281	0	1	0	0	1	No	Yes
1113	1	0	0	0	1	No	Yes
1112	0	1	0	0	0	No	Yes
1190	0	0	1	0	1	No	Yes
1302	0	0	0	1	1	Yes	No
1303	0	0	0	1	1	Yes	No
1314	0	0	0	1	1	Yes	No
1030	1	0	0	0	0	Yes	No
1029	0	0	1	1	1	Yes	No
1166	0	0	0	0	1	Yes	No
1062	0	1	0	0	1	Yes	No
1108	0	0	0	1	0	Yes	No
1304	0	0	1	1	1	Yes	No
1300	0	0	0	1	1	No	Yes
1059	1	0	0	0	0	Yes	No
1301	0	0	0	1	1	No	Yes
1299	0	0	1	1	1	No	Yes
1137	0	0	0	1	1	Yes	No
1194	0	0	0	0	1	Yes	No
1116	0	1	0	0	0	No	Yes
1033	1	1	1	1	1	No	Yes
1000	1	1	1	1	1	No	Yes
1109	0	1	1	1	1	Yes	No
1044	1	0	0	0	1	No	Yes
1181	0	1	1	0	1	Yes	No
1337	0	0	1	1	1	No	Yes
1338	0	0	1	1	1	Yes	No
1279	1	1	1	1	1	Yes	No
1027	1	1	1	1	1	Yes	No
1287	1	0	0	1	1	Yes	No
1009	0	0	1	1	1	No	Yes
1340	0	0	0	1	1	No	Yes
1379	0	0	0	1	1	Yes	No
1342	0	0	0	1	1	No	Yes
1335	0	0	1	1	1	No	Yes
1346	0	0	0	1	1	Yes	No
1113	0	0	1	1	1	No	Yes
1011	0	0	1	1	1	No	Yes
1302	0	0	0	1	1	Yes	No
1314	0	1	1	1	1	Yes	No
1029	0	1	0	1	0	Yes	No
1166	1	0	1	1	1	Yes	No
1062	0	1	1	1	1	Yes	No
1341	0	0	0	1	1	No	Yes
1347	0	0	1	1	1	Yes	No
1339	0	0	1	1	1	Yes	No

TABLE HVIII (CONTINUED)

ID	PER 1	PER 2	PER 3	PER 4	PER 5	Male	Female
1108	0	1	1	1	1	Yes	No
1304	1	1	1	1	1	Yes	No
1323	0	1	0	1	1	No	Yes
1246	1	0	1	1	1	Yes	No
1345	0	0	1	1	1	Yes	No
1300	1	0	0	0	1	No	Yes
1343	0	0	1	1	1	No	Yes
1336	0	0	1	1	1	No	Yes
1344	0	0	0	1	1	No	Yes
1301	0	0	0	1	1	No	Yes
1137	1	0	0	0	1	Yes	No
1191	0	0	1	1	1	Yes	No
1194	0	1	1	1	1	Yes	No
1033	0	1	1	0	0	No	Yes
1109	1	1	1	1	1	Yes	No
1032	0	1	1	1	1	No	Yes
1305	0	0	1	1	1	No	Yes
1403	0	0	0	1	1	Yes	No
1411	0	0	0	0	1	No	Yes
1337	1	1	1	1	1	No	Yes
1338	1	1	1	1	1	Yes	No
1279	1	1	0	1	1	Yes	No
1009	0	1	1	0	0	No	Yes
1288	1	1	0	0	0	No	Yes
1280	0	0	1	1	1	No	Yes
1137	0	0	0	0	1	Yes	No
1379	1	1	1	1	1	Yes	No
1342	0	0	1	1	1	No	Yes
1335	0	0	1	1	1	No	Yes
1113	1	0	1	1	1	No	Yes
1011	0	1	0	0	0	No	Yes
1302	0	1	1	1	1	Yes	No
1314	0	0	1	1	1	Yes	No
1341	0	0	1	0	1	No	Yes
1347	1	1	1	1	1	Yes	No
1339	1	1	0	1	1	Yes	No
1108	0	1	1	0	0	Yes	No
1304	1	1	0	1	1	Yes	No
1246	1	1	1	1	1	Yes	No
1345	0	0	1	1	1	Yes	No
1300	1	0	0	0	0	No	Yes
1343	0	1	0	1	1	No	Yes
1336	0	1	1	1	1	No	Yes
1301	0	0	0	1	1	No	Yes
1191	0	1	1	1	1	Yes	No
1194	0	0	1	1	1	Yes	No
1033	1	0	1	1	1	No	Yes
1109	1	1	1	1	0	Yes	No
1056	1	1	1	0	0	No	Yes